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THE DISTRIBUTION AND ABUNDANCE OF POLAR BEARS (*Ursus maritimus* Phipps) DURING THE ICE-FREE PERIOD IN WESTERN HUDSON BAY

by

ANDREW EDWARD DEROCHER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL 1987

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled THE DISTRIBUTION AND ABUNDANCE OF POLAR BEARS (*Ursus maritimus* Phipps) DURING THE ICE-FREE PERIOD IN WESTERN HUDSON BAY submitted by ANDREW EDWARD DEROCHER in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

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Co-supervisor

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Date October 14, 1987

Abstract

The distribution and movement patterns of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay were studied using a total of 2242 locations of animals of known age and sex collected between 1966 and 1985. Annual patterns of segregation by age, sex, and reproductive status were found. Aspects of learning, intraspecific aggression, habitat selection, foraging, energetic constraints, and physiological parameters were considered to be related to observed patterns.

The high degree of philopatry found was considered to result from learned behaviour, winter distributions of sea ice habitat and seals, and the noncompetitive conditions during the ice-free period that make dispersal of limited benefit. An energy conservation strategy was apparent in movement patterns although many bears moved substantial distances to return to specific sites. The directionality of movement of some animals indicated a significant ability to orientate.

Polar bears on the study area were not uniformly distributed. Some adult males formed aggregations on coastal islands and prominent points. Bears in the aggregations were larger than bears found alone and this was considered possible evidence of a dominance hierarchy based on size. Age and weight were not highly correlated with distribution or movement patterns and were only a factor during some time periods.

In autumn 1985, a Petersen mark and recapture estimate of the population size yielded an estimate of 694 bears, with 95% confidence limits of 535 and 889 between the Churchill and Nelson Rivers. The assumptions of the Petersen method were met or approximated. A population of 734 bears, with 95% confidence limits of 523 and 945, was estimated from strip transect data using Kelker's method. An estimated 103 family groups (S.E.=24) were present during the fall. The number of cubs-of-the-year was estimated at 111 and was similar to the estimated productivity of a population of 700 bears, based on population parameters. Both the Petersen method and the strip transect technique performed well and produced lower coefficients of variation than multi-year

population estimates from other areas.

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The opportunities that are presented to a person during ones life are a function of a complex array of people and circumstances. A particularly special opportunity was presented to me to work on a most impressive animal during this study.

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1. INTRODUCTION

One of the major objectives of ecological studies is to develop an understanding of the patterns and underlying forces that influence the distribution and abundance of species. A complex function of interacting factors, including food availability, habitat suitability, breeding opportunities, and social interactions, influence the dynamics of animal distribution and abundance.

Polar bears (*Ursus maritimus* Phipps) have a circumpolar pattern of distribution in association with the polar ice pack. The distribution of major prey species, ringed seals (*Phoca hispida*) and to a lesser degree bearded seals (*Erignathus barbatus*) (Stirling and McEwan 1975; Stirling and Archibald 1977; Smith 1980), influence the distribution of polar bears. The sea ice is a heterogeneous habitat and the density and availability of seals varies in time and space.

The breeding season of polar bears extends from mid-March to June, with a peak in mid-April to mid-May (Lønø 1970). However, female polar bears only breed every 2 to 3 years, producing a skewed sex ratio of two or three males per oestrous female (Ramsay and Stirling 1986). One product of the scarcity of available females is a high level of competition between adult males for breeding opportunities (Ramsay and Stirling 1986). Competition for food and mating opportunities is intense (Stirling 1974; Ramsay and Stirling 1986) and instances of cannibalism and infanticide (Lunn and Stenhouse 1985; Taylor *et al.* 1985) have been reported. Polar bears, unlike other ursids, do not maintain stable territories and from this it might be expected that their social organization differs from other bears. Polar bears are solitary carnivores and travel and hunt alone for most of their lives. Social units exist in family groups, in which females and cubs can spend over two years together, and in adult breeding pairs for short periods (Ramsay and Stirling 1987). The social organization of polar bears is not fully understood. Adult females are not subordinate to adult males under all circumstances (Stirling 1974; Lunn and Stirling 1985), although females with cubs, particularly

cubs-of-the-year, tend to avoid other bears. Latour (1981b) reported social play in adult male polar bears under non-competitive conditions, a behaviour not reported in other adult ursids (Henry and Herrero 1974).

Polar bears in the southern extent of their range, in Hudson and James Bays, spend several months on land in the late summer and fall when the sea ice melts (Jonkel *et al.* 1976; Stirling *et al.* 1977). The bears spend most of the ice-free period resting and are reported to forage very little (Knudsen 1978; Lunn and Stirling 1985). Once ashore, segregation of the population was noted by Stirling *et al.* (1977) and Latour (1981a). Pregnant females den in the inland areas, give birth to cubs in December or early January, and return to the sea ice in February or March (Harington 1968; Ramsay and Stirling 1982). All other bears return to the sea ice in November or December when Hudson Bay refreezes. The ecological conditions in which polar bears spend the ice-free period are vastly different than those found on the sea ice and competition for resources is limited.

Mammalian social systems can be considered a function of two interacting components: external environmental variables and species parameters (*eg.* morphological and physiological characteristics)(Crook *et al.* 1976). The social organization of group living carnivores has been studied in several species (*eg.* wolves (*Canis lupus*) (Mech 1970); lions (*Panthera leo*) (Schaller 1972); spotted hyena (*Crocuta crocuta*) (Kruuk 1972)). However, the social organization of solitary carnivores is not as well understood. This study examines some aspects of the ecology of the polar bear under a set of environmental variables that result in low levels of competition.

The first paper of my thesis deals with the distribution, movement patterns, and philopatry of polar bears during the ice-free period. Bears of different age, sex, and reproductive classes were compared for differences in distribution and movement over the ice-free period. The primary objectives of this study were to quantify the patterns of distribution, movement, and fidelity, with a consideration of the causes and consequences

of observed patterns. Variables such as age and weight were considered as possible factors influencing distribution patterns.

Despite the vast differences in the ecological conditions between the sea ice and terrestrial habitats used by polar bears, some distinct similarities have been reported. For example, spatial segregation of adult females with cubs occurs both on the sea ice and on land (Stirling *et al.* 1977; Stirling *et al.* 1981). The first paper considers various aspects of the natural history of polar bears on the sea ice and relates them to those seen on land. Some aspects of the behavioural ecology of polar bears are examined relative to the different age and sex classes present in the population.

Animal distribution and abundance are "but the obverse and reverse aspects of the same problem" (Andrewartha and Birch 1954). The size of polar bear populations are extremely difficult to estimate and to date only multi-year estimates have proven of any utility (*eg.* DeMaster *et al.* 1980; Furnell and Schweinsburg 1984; Amstrup *et al.* 1986). Polar bears are generally distributed at low densities on the sea ice and are therefore difficult and expensive to locate. The second paper deals with estimating the size of the population of polar bears in western Hudson Bay, during the ice-free period, when the density is higher than is found on the sea ice. The Petersen mark and recapture estimate (Seber 1982) was used to obtain a single-season estimate of the total population size and the number of cubs present during the fall. The assumptions of the Petersen method are analyzed using natural history information and statistical tests to determine the effects of possible biases. A second estimate of the population size was made using strip transect methods. The methods of estimating population size are compared and the relative merits of each method are discussed.

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2. DISTRIBUTION AND MOVEMENT PATTERNS OF POLAR BEARS (*Ursus maritimus* Phipps) DURING THE ICE-FREE PERIOD IN WESTERN HUDSON BAY

2.1 Introduction

Animal migration is generally considered to be the movement of an animal that allows it to piece together a series of partial habitats to produce a 'life-track' (Southwood 1983). Much of the early research on animal movements was related to foraging strategies and the distribution of food resources (MacArthur and Pianka 1966; Emlen 1966; Charnov 1976; Pyke 1983). The importance of social organization, territoriality, and mating systems in animal distribution have also been considered of primary importance (Wynne-Edwards 1962; Brown 1964; Krebs 1971; Clutton-Brock and Harvey 1977; Greenwood and Swingland 1983). The net result is that migration can be considered a mechanism through which animals can improve their long-term reproductive success (Baker 1978; Sinclair 1983). Migration is thought to have evolved in temperate regions as a mechanism to avoid a resource bottleneck induced by seasonal climatic changes (Lack 1954; Baker 1978). Sinclair (1983) argued that migration evolved as an adaptation to finding better food resources for breeding. Polar bears (*Ursus maritimus*) in Hudson Bay undergo a seasonal migration, moving from the sea ice onto land, that for most individuals is not related to either the acquisition of food or breeding opportunities, but rather to the loss of the sea ice habitat as it melts away during the summer.

Polar bears have a circumpolar distribution closely tied to the arctic pack ice (DeMaster and Stirling 1981). They are solitary carnivorous mammals preying predominantly upon ringed seals (*Phoca hispida*) and secondarily on the larger, but less abundant, bearded seal (*Erignathus barbatus*) (Stirling and Archibald 1977; Smith 1980).

The world population of polar bears is an assemblage of smaller sub-populations which show fidelity to given areas (DeMaster and Stirling 1981; Stirling *et al.* 1975; 1977;

1980; 1984; Jonkel *et al.* 1976; Schweinsburg *et al.* 1982; Furnell and Schweinsburg 1984; Lentfer 1983; Larsen *et al.* 1983; Amstrup *et al.* 1986). The polar bears in western Hudson Bay are a relatively discrete sub-population of a larger population occupying the whole of the Bay. During July and early August each year the bears in this area are forced ashore as the sea ice melts. They remain onshore throughout the summer and fall until the sea ice reforms in November or December. Polar bears were observed along coastal areas in Manitoba as early as 1619 when the Danish explorer Jens Munk reported polar bears near the mouth of the Churchill River during September (Gosch 1897). In the mid 1700's, Samuel Hearne reported seeing polar bears along the coast during the summer and noted their absence during the winter (Hearne 1795). Hearne also noted that pregnant females spent the winter in dens along the tree-line and gave birth on land to an average of two young.

Russell (1975), Knudsen (1978), and Lunn and Stirling (1985) reported that polar bears feed little during the time spent on land in western Hudson Bay and that the total intake is probably energetically insignificant. The dominant energy source used by bears during their time on land is fat deposited during the previous spring while hunting seals on the sea ice. Ramsay (1986) found that the ratio of serum urea to creatinine found in polar bears during the summer was similar to that found by Nelson *et al.* (1984) in black bears (*Ursus americanus*) during hibernation. Ramsay (1986) hypothesized that polar bears may be in a physiological state similar to that shown by black bears and grizzly bears (*U. arctos*) during hibernation. While on land, polar bears are relatively inactive spending approximately 70 to 90 percent of their time resting (Latour 1981a; Lunn and Stirling 1985).

Stirling *et al.* (1977) and Latour (1981a) noted a spatial and temporal segregation of polar bears during ice-free periods in western Hudson Bay. They noted that adult males were found along the coastal areas, adult females with and without cubs were distributed further inland, and subadult age classes were found between. Aggregations of

adult males at certain localities along the coast were reported by Knudsen (1973) and Stirling *et al.* (1977). A large concentration of polar bears, believed to be a function of ice formation patterns that allows the bears earlier access to the sea ice in the fall, occurs each fall in the Cape Churchill area (Stirling *et al.* 1977; Latour 1981a). Black and grizzly bears have permanent territories that overlap with conspecifics of similar and different age and sex classes (Craighead 1976; Young and Ruff 1982; LeCount 1980; Jonkel and Cowan 1971; Pearson 1975). In contrast, polar bears do not set-up permanent territories due to the labile nature of the sea ice which influences the distribution of food resources. During winter, polar bear populations are segregated by age, sex, and reproductive class because of preferences for different ice types (Stirling *et al.* 1981).

The breeding season occurs while polar bears are on the sea ice in late March through to mid-July (Lentfer *et al.* 1980; Lønø 1970). Polar bears display delayed implantation (Uspenski 1977; Lønø 1972; Wimsatt 1963). Pregnant females that have gone onto land during the ice-free period do not return to the sea ice after freeze-up, but remain inland and dig dens, giving birth to cubs in late December or January and returning to the sea ice from February through April (Harington 1968; Stirling *et al.* 1977; Ramsay and Stirling 1982; Ramsay and Andriashek 1986). One of the most concentrated regions of polar denning known in the world lies south of Churchill, Manitoba (Jonkel *et al.* 1972; Stirling *et al.* 1977). Polar bears in this area have a larger litter size and a shorter breeding interval than is seen in other parts of their range (Stirling *et al.* 1977; Ramsay and Stirling 1982). As approximately 40 percent or more of the adult females have a two year breeding interval, many cubs are weaned before the age of 1.5 years. Females also exhibit a three year breeding cycle, typical of higher latitude populations, and therefore are accompanied by yearling cubs during the summer.

Polar bears, unlike other ursids, may undergo long seasonal migrations. As the breeding season is over and food resources are believed to be limited or non-existent

while polar bears are on land, the factors influencing the summer and fall distribution of polar bears are unclear. Few studies have detailed the behavioural ecology of solitary carnivores in any circumstances. This study investigates and quantifies the distribution and movement patterns of polar bears, under non-competitive conditions during their summer migration, and examines possible factors contributing to the observed patterns.

2.2 Materials and Methods

2.2.1 Study area

Hudson and James Bays together comprise one of the largest inland seas in the world. Hudson Bay is shallow with an average depth of less than 100 m and is frozen over from November to late July each year with the ice reaching a maximum extent in January through April (Larnder 1968). The Bay is never 100 percent ice covered as an extensive shore lead parallels the coast between the shore fast ice and the free floating ice, in deeper waters, further offshore (Larnder 1968). Numerous smaller leads penetrate far into the central regions.

The study area extended from the mouth of the Nelson River (57° N latitude) to the mouth of the Churchill River (58° 45' N latitude) and between the coastline west of longitude 92° 25' W and inland to 94° 15'W, which corresponds roughly to the extent of westward movements seen during the ice-free period (Figures 2-1 and 2-2). The area is collectively known as the Hudson Bay Lowlands (Ritchie 1960) and is an extensive peatland along the boreal forest-tundra ecotone between the true arctic tundra and the sub-arctic open boreal forest (taiga) (Hare 1950; Thompson 1968).

Hudson Bay lies in the central part of the Canadian Shield and the quaternary geological history of the area was important in shaping the local geography (Lee 1968; review by Shilts 1982). At the decline of the last glaciation, 7000-8000 year ago, the Tyrell Sea inundated the depression formed by downwarping during glacial occupation. Isostatic rebound has resulted in its contraction into the present bounds of Hudson Bay. The area evacuated by the Sea is generally flat with elevations ranging from sea-level to about 300 m ASL with a gradual east-west incline. The area is underlain by horizontally bedded limestone with a thick mantle of glacial and marine clay, the latter responsible for the poor drainage patterns and subsequently the existence of peat-forming vegetation types over much of the area (Ritchie 1962). Relief is provided by numerous raised

beaches and extensive eskers attesting to an active glacial and marine history. The study area is dotted by numerous small lakes and ponds and poorly defined dendritic drainages flowing east into the Bay. Continuous permafrost is found in the northern portion of the study area and grades into discontinuous permafrost further south (Ritchie 1962). Permafrost is an important factor influencing the distribution and productivity of plant species and communities in the area.

The study area is characterized by a typical arctic climate that is strongly dependent upon changes in the state of surface waters in Hudson Bay (Thompson 1968). The winters lasting from November to May are long, cold, and dry. A general warming trend is present by late May and grades into a brief spring. With the advent of a rapidly increasing day length, the ice in the Bay begins to break-up and is ice-free by mid-August. The cloud cover increases from a winter low of 40-50 percent to 60-70 percent during the summer. Summers are cool and wet lasting the brief two or three months in which the tundra is free of snow. Coastal areas are often shrouded by fog and have lower temperatures than inland areas with less fog (Thompson 1968). Mean monthly temperatures for June, July, and August are 5.8° C, 12.0° C and 11.6° C, respectively (Canada Atmospheric Environment Service 1973). Warm air masses moving northward from the Gulf of Mexico can often raise daytime temperatures to above 25° C (Robinson 1968).

By September and October, cloud cover reaches a maximum of about 80 percent; temperatures drop and storm activity increases. Mean monthly temperatures for September, October, and November are 5.7° C, -1.1° C, and -11.7° C, respectively (Canada Atmospheric Environment Service 1973). The fall is brief and merges quickly with winter as cold arctic air masses advance and the day length decreases.

The ice in Hudson Bay is characterized by extreme variability with patterns of ice formation and break-up differing considerably between years and localities (Larnder 1968; Danielson 1971). The formation of new sea ice begins along the Keewatin coast north

of Rankin Inlet and moves southward forming a rim of ice several kilometers wide. The ice eventually extends south to Cape Churchill, usually by the first or second week of November. Within weeks the ice covers most of the Bay. The timing and pattern of break-up appears to be more variable than ice formation patterns. Of particular importance to polar bears is the position of large ice pans late in the break-up season. In general, the last of the major ice floes occur off the coast of Manitoba and Ontario, possibly a function of the counter-clockwise circulation pattern in the Bay.

Ritchie (1960) divided the Hudson Bay Lowlands into four dominant vegetation zones: the transition zone, the moss-muskeg type, the treeless bog, and the lowland complex. He identifies eleven community types within these zones. Much of the following is derived from Ritchie (1960; 1962).

The transition zone lies along the western edge of the study area and is largely comprised of a moss-muskeg community seated on deep peat (60-200 cm). Open stands of depauperate black spruce (*Picea mariana*) associated with *Sphagnum* mosses, various ericoid shrubs, willows (*Salix* spp.), and dwarf birch (*Betula glandulosa*) are interspersed throughout the area. Heath and string bogs, found in wetter locations, are dominated by Labrador-tea (*Ledum groenlandicum*), *L. decumbens*, crowberry (*Empetrum nigrum*), mosses (*Sphagnum* spp.), and reindeer lichens (*Cladonia* spp.) Areas of higher elevation bear open coniferous forest of black spruce, white spruce (*P. glauca*), tamarack (*Larix larciana*), and poplar (*Populus balsamifera*).

East of the transitional zone lies the moss-muskeg zone founded on deep peat. The area is flat with dendritic drainage patterns and exhibits a moderate number of ponds. The moss-muskeg community dominates the zone with willow, birch, and alder (*Alnus* sp.) forming a dense growth along watercourses.

The central portion of the study area is dominated by the treeless bog types characterized by very poor drainage, numerous small lakes and ponds, and the occasional gravel or sand ridge. Palsa, string, and heath bogs are common throughout with a

smaller moss-muskeg component. Mosses, lichens, *Vaccinium* spp., sedges, and *Ledum* spp. are the dominant species with conifers found along the rivers and streams where sufficient mineral soil exists.

The coastal area is a flat strip up to about 20 km inland. It is part of the lowland complex and is a mosaic of numerous communities. Bogs and fens dominate the wetter areas several kilometers inland. Scrub willow and birch are common and frequently ring small lakes and ponds. In the southernmost areas, open coniferous forest dominated by black spruce, is found along the coastline. Further north, larch fens are common, but in the area of Rupert Creek the tree line moves away from the coast. Northern coastal regions and islands are dominated by sedge-grass-herb meadows, composed of various sedges and grasses (*Elymus* spp., *Poa* spp., and *Puccinellia* sp.), with extensive salt marshes and shrubs communities occupying discrete areas lying parallel to the coast. The beach areas are dominated by coarse gravels and sand in the northern regions and by finer clay materials along the coast south of Rupert Creek. Extensive tidal flats are exposed several kilometers offshore at low tide.

Areas inhabited by humans are found only in the north-west corner of the study area near Churchill, Manitoba. Human activity throughout the area is generally localized and limited to various research activities and very light tourist use in the late fall.

2.2.2 Methods

Polar bear tagging studies began in western Hudson Bay in 1966 and have continued to date. The objectives, methods, and intensity of tagging operations performed by the Canadian Wildlife Service (CWS) and Manitoba Department of Natural Resources (MDNR) have varied from year-to-year. Polar bears were captured using a variety of methods. Most animals were immobilized from a Bell 206B helicopter using remote injection equipment (Cap-Chur, Palmer Chemicals Ltd., Douglasville, Ga.). Techniques followed those outlined by Lentfer (1968) and Larsen (1971) with modifications as in Ramsay *et al.* (1985) and Haigh *et al.* (1985). Some bears were captured in Aldrich leg snares, culvert traps, or darted from a motor vehicle (Jonkel 1967; Stirling *et al.* 1977; Ramsay *et al.* 1985).

Once the bears were fully immobilized a set of standardized parameters were recorded and specimens were collected. A plastic eartag was placed in each ear and tattoos applied to both upper lips with a unique number to facilitate long-term identification of individual animals. A vestigial or rudimentary premolar tooth was extracted from all bears greater than one year old. Extracted teeth were thin-sectioned following methods outlined by Thomas and Bandy (1973) and Stirling *et al.* (1977) and the age determined from counts of cementum annulation rings. Canine eruption patterns and body size were used to determine cubs-of-the-year. Morphometric measurements including axillary girth, straight-line length, and maximum skull length and width were collected. Weights of polar bears were estimated from a cattle weight tape based on the relationship between scale weights and weights derived from the tape (Stirling *et al.* 1977). The sex and reproductive status of each animal was recorded. Blood samples from the femoral vein were collected from some bears to obtain information on serum testosterone and progesterone levels. Testosterone levels were analyzed by Dr. R. Nelson and S. Palmer at the Carle Foundation Hospital, University of Illinois, Urbana. The serum testosterone data used in this study are modified from those used by Palmer *et*

al. (1986). Serum progesterone levels were determined at the Reproductive Endocrine Laboratory of the University of Saskatchewan and were used as an aid to pregnancy detection as outlined by Ramsay (1986).

To allow the identification of animals from a distance, large (30 cm high) letters or numbers were painted on the backs or sides of each bear using an indelible black dye (Nyanzol). A total of 89 eartag, glue-on, and neck collar radios were placed on randomly selected animals of different age, sex, and reproductive classes during 1984 and 1985. The more powerful radio collars were used predominantly on lone adult females as the extra range was necessary to locate animals in earth dens. Prior to the ice-free period of 1984, seventy-seven bears throughout the study area were radio tagged as part of other studies. Due to differences in study objectives, the frequency of radio locations during this earlier period was not as high as during the 1984-1985 study.

The capture period varied yearly and began as early as mid-July and continued as late as December. Helicopter captures were performed primarily in July and August in most years. During 1984 and 1985, the main study objectives included an investigation into the distribution and movement patterns of polar bears on land during the ice-free period. Helicopter capture sessions extended from July 21 through August 27 and from July 26 through September 1 for 1984 and 1985, respectively. In 1984, capture effort was centred along the coastal regions in an attempt to mark and radio bears as soon as they arrived on land. The sampling design in 1985 was modified to a stratified random sample based on known distribution patterns. Some information collected during September 1986 was included in some analyses.

In order to obtain successive locations of known animals throughout the ice-free period, fixed-wing aerial surveys and aerial radio-tracking surveys were conducted over the study area every two weeks during 1984 and 1985, depending on weather conditions and aircraft availability. Radio tracking surveys were flown at elevations between 1500 m and 3000 m using Cessna models 180, 185, 206, and 337 aircraft with strut mounted

H-antennae. Radio tagged animals were visually observed only on alternate occasions, due to the time necessary to drop sufficient altitude and to reduce possible disturbance, to ensure radios were attached and that accompanying cubs were still present. Surveys to resight marked bears were flown at 100 m above ground level. During 1984, aerial surveys were used predominantly to relocate radio tagged animals. In 1985, random strip transects were flown over the study area to provide a population estimate (Chapter 3). All locations of known bears were recorded to the nearest minute of longitude and latitude. Flights to relocate marked and radio tagged animals were flown on August 25-26, September 6, 11, 12, and 26-28, October 15 and 17, and November 6-7 in 1984. In 1985, survey flights were flown on September 4-7, 20-23, and 30, October 1-3, 5, 17, and 18, and November 2-4. Resightings of marked bears were also obtained from MDNR staff and other reliable observers working in the area.

During March 10-14 1985, a radio tracking survey was conducted over the sea ice to obtain information on the winter distribution of polar bears. The survey was flown with a Cessna 337 aircraft at an elevation of 3000 m. It was possible to observe only two of the radio tagged bears due to the time and fuel necessary to descend from the surveying altitude. The area covered extended from the Manitoba-Ontario border north to Rankin Inlet, Northwest Territories, and offshore up to 350 km.

During the fall of most years, a large influx of adult females with cubs and subadults move into the area near the Churchill townsite and these animals comprise the dominant portion of the sample prior to 1977 (Stirling *et al.* 1977; Lunn and Stirling 1985). After 1977, the region sampled increased and by the 1980's animals were captured throughout the study area. Nearly sixty percent of all polar bear handlings have occurred since 1980.

For the purpose of analysis, all bears were placed into one of five groups: family groups (adult females five years and older accompanied by cubs-of-the-year or yearlings), lone adult females (five years and older), subadult females (independent bears

one to four years old), adult males (five years and older), and subadult males (independent bears one to four years old). The separation between adult and subadult animals is based on the onset of reproductive maturity (Stirling *et al.* 1977; Ramsay 1986). Females in the study population appear to begin to reproduce between four and five years of age (Ramsay and Stirling 1982, 1987). Fifty percent of the five-year-old females, but only five percent of four-year-olds, handled in the study area are associated with cubs. No three-year-olds have been caught with cubs. Within the category of subadult females, 14 percent of the sightings were from bears in the four-year-old age class. Although it was possible that some of these animals were pregnant, at least 38 percent of the four-year-olds did not appear to be pregnant, based on resightings in the following year and it was felt that including these animals in the subadult group was valid. The onset of spermatogensis in grizzly bears occurs at approximately five years of age (Pearson 1975). The age at which male polar bears mature is unknown, but is believed to be similar to that of grizzly bears. In order to be consistent between sexes, the age of sexual maturity was considered to be five years of age for both groups, although the actual onset of breeding may vary between the sexes. Ramsay (1986) reported that 83 percent of lone adult females in the study population demonstrated elevated serum progesterone levels indicative of pregnancy and therefore all lone adult females were pooled into the same group.

As the methods in which data were collected varied considerably from year-to-year, it was necessary to remove some data points from the analysis. Multiple resightings or captures of bears at the Churchill dump and townsite within a single year were not included in any of the analyses pertaining to distribution and movements, although the initial sightings of individuals were used. There was a bias towards the capture of bears in the northern section of the study area in samples prior to 1980. During 1984 and 1985, efforts were made to sample the whole study area.

During September 1986, a sample of scats were collected from known bears with the objective of determining possible forage species during the fall, particularly in the inland areas. All scats were frozen and then washed through a series of screens. The species composition of a scat was estimated by examining a series of random samples from each screening with the aid of a binocular microscope in a manner similar to that outlined by Russell (1971). As each scat was analyzed, the volume of each component was estimated and placed into one of six volume classes: trace(tr)-5%; 5-25%; 25-50%; 50-75%; 75-95%; 95-100%. Species identification was based on a comparison of the leaves and seeds from a reference collection to the samples obtained from each scat. Grasses (Family Gramineae) and sedges (Family Cyperaceae) were not separated and were grouped under the heading of graminoids-cyperaceae. Mosses were not keyed to species or genus.

All data were analyzed using BMDP (Department of Biomathematics, The University of California, Los Angeles) statistical software. To quantify the distribution patterns of polar bears during ice-free periods, each location of an animal was described as the shortest distance from the coast. The coastline was considered to be the entry point between habitats: the sea ice and the land. The use of distance from the coast was selected as it was thought to be an unbiased parameter through which the distribution of the bears could be quantified. This measure is a uni-dimensional parameter of a two dimensional distribution and does not consider the north-south distributional aspects. However, it did allow for meaningful comparisons to be made between groups. In the analysis of distance moved per day and direction moved, only relocations of animals made within thirty days (approximately two times the survey interval) were used. The data were grouped by month and movement information was allocated to the month in which the midpoint between relocation dates occurred. The analysis of direction of movement was further constrained to observed movements of two kilometers and greater, as movements less than this were considered within the range of

accuracy of mapping in some habitat types.

Non-parametric tests were used for most comparisons as data could not be normalized using standard transformations. Comparison of distance from the coast and distance moved per day data were analyzed using the Kruskal-Wallis test and the Mann-Whitney *U*-test (Conover 1980; Sokal and Rohlf 1981). The Kruskal-Wallis non-parametric multiple comparison test was used to determine which groups differed for those analyses with significant Kruskal-Wallis results (Conover 1980). The distance from the coast and the distance moved per day by families with cubs-of-the-year and those with yearlings were compared using the Mann-Whitney *U*-test to determine if differences in movement patterns existed. To assess the influence of bias in the data over all years, the information from radio tagged bears in 1984 and 1985 was compared to all other sightings and capture data for animals of each group. The information from radio tracking in 1984 and 1985 was considered to be less liable to bias given the distribution of capture and the frequency and methods of relocation. Kendall's coefficient of rank correlation test was used to determine if age or weight of a bear was a factor related to the distribution or movements of animals within a group and thereby accounting for some of the observed variability (Sokal and Rohlf 1981).

Directional data were analyzed using circular statistic methods as outlined by Batschelet (1981). The mean vector length (r) was used as a measure of concentration in describing circular distributions. Values can range from 0, indicating a non-orientated distribution, to 1, which describes a distribution along a single direction. The bearing of the mean vector was calculated for each group and the Rayleigh test was used to determine if the orientation of the sample differed significantly from a random distribution (Batschelet 1981). Where visual inspection of plotted data indicated a strong bimodal distribution in the orientation patterns, an axis of orientation (*ie.* orientation along a line rather than a single bearing) was determined and is presented for those samples.

Site fidelity of polar bears was examined on three different scales and time frames. General fidelity to western Hudson Bay was examined using mark and recapture studies and harvest tag returns from Inuit communities. The second level of analysis was based on a smaller scale and investigated the fidelity patterns of polar bears within the study area on a monthly basis between years. To determine the degree of fidelity shown over time the distance between all known locations of a bear in a single ice-free period and its positions a year or more later, during the same month, was determined. This was done for adults, subadults relocated as adults, subadults relocated as subadults, and cubs relocated as independent bears. Values were calculated including and excluding harvest information. Finally, I analysed movement patterns and fidelity or degree of emigration from the study area during a single ice-free period.

Probability values (P) associated with statistic tests represent the two-tailed probability level. The level of significance was set at $P \leq 0.05$ unless specified otherwise.

2.3 Results

In the course of polar bear studies over the last nineteen years, 1340 captures and 902 resightings of independent animals have taken place in the study area during the period that the bears are on land in the summer and fall (Table 2-1 and Figure 2-3). Known individual polar bears were resighted or recaptured with an average interval of 19.5 days (S.E.=0.8; n=1201) during the ice-free period. Using only animals relocated with an interval of thirty days or less produced a mean relocation interval of 7.2 days (S.E.=0.3; n=913).

2.3.1 Distribution of polar bears

Figures 2-4 to 2-8 show the distribution of each group, by month, for bears located between 1966 and 1985. Table 2-2 shows the monthly mean, median, and range for the distance from the coast for each group of polar bears. Representatives of all five groups could be found along the coast throughout the study period and therefore the range is equal to the maximum distance from the coast. In general, the animals were not distributed at random, but showed a continuous asymmetric distribution highly skewed to the west for most periods. In unimodal asymmetric distributions the mean is usually closer to the drawn-out tail of the distribution than is the median (Sokal and Rohlf 1981).

The distribution of some groups of bears about the study area is highly clumped during certain periods. Adult males demonstrated a tendency to form loose aggregations at prominent points and small islands along the coast. Although animals in an aggregation were defined broadly as being less than 100 m apart, individuals were often located within 1 or 2 m of each other. Adult males in an area would sometimes congregate even more closely upon the approach of the helicopter and move off in a group of 3 or 4, touching shoulders as they walked or ran. The size of the aggregations ranged from 2 to 14 individuals and the age of known animals ranged from 5 to 20

years in both 1984 and 1985. The age and weight of individuals seen in an aggregation, during August and September, was compared to those bears sighted alone. Only data for 1984 and 1985 were compared due to the more intensive coverage of the area before the period of late fall aggregation at the Cape Churchill area. Of the adult males captured, 52 percent (32/61) and 54 percent (20/37) were seen in aggregations at least once during 1984 and 1985, respectively. Of the 19 adult males captured in both years, 3 were seen alone in both years, 10 were seen in aggregations in both years, and 6 were seen in an aggregation in one year and alone in the other. Adult males sighted in aggregations during 1984 had a mean age of 12.7 years (S.E.=0.9; n=32), not significantly different from those bears seen alone with a mean age of 11.8 years (S.E.=0.9; n=29; t_{59}= -0.69; P=0.495). Adult males sighted in aggregations were significantly heavier ($\bar{X}$=403 kg; S.E.=15; n=32) than those sighted alone ($\bar{X}$=343 kg; S.E.=15; n=29; t_{59} = -2.74; P=0.008) in 1984. A similar pattern was observed in 1985. There were no differences in the mean age of adult males in aggregations ($\bar{X}$=14.9 years; S.E.=1.1; n=20) and adult males seen alone ($\bar{X}$=12.4 years; S.E.=1.2; n=17; t_{35}= -1.56; P=0.127). However, there were significant differences in the mean weights, with aggregating adult males averaging 391 kg (S.E.=16; n=20) and those seen alone averaging 329 kg (S.E.=19; n=17; t_{35}=*-2.51; P*=0.017).

Some aggregation areas were used over several years, while others were used only occasionally. For example, a prominent spit 11 km south of the Broad River was used regularly throughout the summer until late in the fall. The spit consistently had several residents, some of which spent over 4 weeks at the spot. A less pronounced point 22 km NNW of the Broad River regularly had an aggregation of between 5 and 9 adult bears during 1984, but was only used by single bears during 1985 and 1986. Subadult males were occasionally seen in aggregations of adult males, but subadult females were only seen nearby (*eg.* 300 m). Family groups, lone adult females, and subadults were generally found independent of other bears until late in the fall when high densities of

all age and sex classes were common at Cape Churchill and the Churchill dump, although the dump is dominated by families and subadults and the Cape by adult males.

Sample sizes obtained for each month and for each group varied considerably and reflect differences in the conditions under which the data were collected in different years. Insufficient samples in some years precluded a detailed analysis of annual differences in distributional patterns. During 1984 and 1985, enough data were collected to permit the investigation of annual differences in the distribution. Table 2-3 gives the monthly mean distance from the coast for all groups for both years and the Mann-Whitney *U*-test results for differences between the years. The results of this analysis indicated that significant variation in the annual distribution of polar bears occurred for 4 of 24 comparisons made. The September locations of lone adult females and subadult males and October locations of adult males were significantly further inland during 1985 when compared to 1984. Adult females with cubs were significantly closer to the coast during November 1985 than during 1984. No significant differences were found between the mean age or mean weights of a group between 1984 and 1985 (Table 2-4). Overall, the analysis indicated that annual variability, although present, was not of a magnitude that introduced serious confounding of the overall trend in distribution and therefore, pooling years was valid.

During July, the period that bears arrive onshore, there were no significant differences in the distribution of the different groups (Kruskal-Wallis $H=6.88$; $P=0.142$; df$=4$). Significant differences in the distance from the coast occurred during August (Kruskal-Wallis $H=88.01$; $P<0.001$; df$=4$), September (Kruskal-Wallis $H=82.14$; $P<0.001$; df$=4$), October (Kruskal-Wallis $H=267.80$; $P<0.001$; df$=4$), and November (Kruskal-Wallis $H=49.77$; $P<0.001$; df$=4$). Table 2-5 shows the multiple comparison of the groups for August through November. Family groups and lone adult females were spatially segregated from adult males from August through November and from subadults of both sexes from September through November. Families and lone adult

females occupied different areas only during October. During November, families were not spatially segregated from lone adult females because of the distribution of non-pregnant lone adult females closer to the coast. Subadult males and females were spatially segregated from adult males only during August. Female and male subadults were spatially separated only during October when subadult males were closer to the coast.

Table 2-6 shows the mean, median, and range of bears located by radio tracking only. Significant differences were found in 7 of 20 comparisons made between the distribution of the bears, as determined by radio tracking in 1984 and 1985 and from all other location sources (Table 2-7). The source of these differences may be a function of the method of collection or related to differences in the number of individuals included in the two samples. The major differences in the distribution of adult males between the two methods of data collection may have been a function of putting radios on adult males already in the inland area. Alternatively, the differences may reflect a bias in the data that represents over sampling in the coastal region. There is a high degree of variability in the behaviour of individuals in the population and the smaller number of bears radio tagged may not fully reflect patterns in the population or possible annual variability that may exist.

Using radio-tracking data, variation in the distance from the coast was found between groups during August through November (Kruskal-Wallis $H=14.59$; $P=0.006$; df$=4$), (Kruskal-Wallis $H=20.63$; $P<0.001$; df$=4$), (Kruskal-Wallis $H=33.56$; $P<0.001$; df$=4$), and (Kruskal-Wallis $H=26.98$; $P<0.001$; df$=4$), respectively. Table 2-8 shows the results of the multiple comparisons of groups from August through November. When comparing Tables 2-5 and 2-7, 27 of 40 comparisons yield the same interpretation with respect to the differences or similarities in the distribution patterns and the general pattern of the two analyses remains the same. Major differences were found in the comparison of subadult males and family groups, but may be a function of

the small number of radio tagged bears. Only 17 subadults were radio tagged during 1984 and 1985, while 165 other animals were included in Table 2-5. Based on the overall similarity in the two analyses and the larger data base in the total sample, it was felt that the inclusion of all data better represented the patterns of distribution.

Adult females with cubs-of-the-year and adult females with yearlings showed no significant differences between their distribution patterns (Table 2-9). As the spatial and temporal distribution patterns of the two groups were similar, their pooling into a single group was considered valid.

All groups of polar bears showed highly significant differences in their distribution on a monthly basis (Table 2-10). The general pattern illustrated by family groups, subadult females, adult males, and subadult males was that animals tended to be near the coast in July with subsequent movement inland, reaching a maximum in August or September. The timing of the return to the coast differed between groups and within groups. The departure of the subadults from the inland area in August occurred first. The magnitude of the distance from the coast between months varied considerably between the different segments of the population. The movement patterns of lone adult females differ from all other groups because pregnant females remained inland to give birth to young.

The lone adult females that remained along the coast, or returned there during October and November after being inland, represented approximately 22 percent (22/100) of the total found in the study area from 1966-1985. Five of those females were five years old and two were older than 21 years. Serum progesterone levels of 0.1 ng/ml for two of the females indicated that they were not pregnant. The lone adult females found within 10 kilometers of the coast during October were significantly lighter in weight ($\bar{X}$=173 kg; S.E.=9; n=13) than adult females further inland ($\bar{X}$=224 kg; S.E.=9; n=51; t_{62}=-2.77; P=0.007) although, they were not significantly different in average age ($\bar{X}$=9.8 years; S.E.=1.6; n=13) from females found further inland ($\bar{X}$=12.8 years;

S.E.=0.9; n=51; t_{62}=-1.61; P=0.113). During November, there were still significant differences between the mean weight of lone adult females within 10 km of the coast ($\bar{X}$=156 kg; S.E.=14; n=16) and those further inland ($\bar{X}$=223 kg; S.E.=11; n=19; t_{33}=-3.76; P=0.007). However, there were no significant differences in the mean ages between bears near the coast ($\bar{X}$=11.6 years; S.E.=1.7; n=16) and those in the inland areas ($\bar{X}$=10.3 years; S.E.=1.3; n=19; t_{33}=0.62; P=0.542).

The weights of animals after capture were estimated from the rate of weight loss observed in bears captured early in the study period and subsequently recaptured later in the fall. The mean rate of weight loss observed was 0.96 kg per day (S.E.=0.26; n=22) pooled for all independent animals greater than one year old. This method, while a simplification of reality, was considered adequate to provide an approximate weight of study animals throughout the study period.

Significant correlations between age and weight were found to be only weakly correlated with an animal's distance from the coast indicating that neither age or weight were strongly related to the distribution of polar bears within each group (Table 2-11).

2.3.2 Distance moved per day

The distance moved per day provides an approximate measure of activity, but does not accurately describe the details of movements. It was not possible to ascertain if movement occurred sporadically in short bouts of longer distance or if it was a continuous process of shorter movements.

The data collected in 1984 were compared to those of 1985 in an attempt to determine the degree of annual variability in movement patterns. Insufficient data from years prior to 1984 precluded a longer-term analysis of movement patterns. The only significant difference (P=0.043) detected between 1984 and 1985 was for adult males in August (Table 2-12). Based on the analysis of information collected in 1984 and 1985, the pooling of all information across years was considered valid.

Table 2-13 presents the mean, median, and range of distance moved per day for each group over the five months of the study. Samples were small for the month of July due to lower research activity and were not analyzed. Significant variation in distance moved per day was found during August (Kruskal-Wallis $H=11.40$; $P=0.022$; df=4) and November (Kruskal-Wallis $H=12.97$; $P=0.011$; df=4). No variation was found during September (Kruskal-Wallis $H=6.66$; $P=0.155$; df=4) and October (Kruskal-Wallis $H=7.25$; $P=0.123$; df=4). The Kruskal-Wallis multiple comparison test results only revealed significant differences in movement patterns between subadult females and subadult males (Table 2-14). The multiple comparison test did not detect differences between any of the groups during August, although subadult females and adult males were significantly different at the $P\leq 0.10$ level (*ie.* critical Z value of 2.58). Removal of suspected non-pregnant females from the lone adult female group resulted in significant variation between groups during August (Kruskal-Wallis $H=11.02$; $P=0.0264$; df=4), October (Kruskal-Wallis $H=11.41$; $P=0.022$; df=4), and November (Kruskal-Wallis $H=18.00$; $P=0.001$; df=4), but not during September (Kruskal-Wallis $H=6.25$; $P=0.181$; df=4). Table 2-15 shows the multiple comparison results which did not detect differences during August and October, despite the significant Kruskal-Wallis test. During November, pregnant females were found to move less than subadult females. The results of all other comparisons were the same. No significant differences were found in the distance moved per day between adult females with cubs-of-the-year and females with yearlings (Table 2-16).

Family groups, subadult females, and adult males differed significantly between months in the mean distance moved per day (Table 2-17). These three groups moved less in September than either before or after this time. The monthly mean distance moved per day did not vary significantly for lone adult females and subadult males. However, when non-pregnant females were removed from the lone adult female group, there was significant variation (Kruskal-Wallis $H=8.73$; $P=0.033$; df=3) in the monthly

values of distance moved per day with minimum levels of movement during November.

Significant, but weak correlations between distance moved per day and age were found in only 2 of 21 tests using Kendall's rank correlation test (Table 2-18). Significant correlations were found with weight and distance moved per day for 3 of 21 tests (Table 2-18).

Sufficient data were available to qualitatively examine movement patterns of some individual bears between 1984 and 1985, although statistical analysis of the data was confounded by differences in the sampling dates between years. Most of the information available was from adult males due to their relatively higher visibility along the open coastal regions and subsequent sighting by casual observers. The mean distance moved per day in successive years, weighted by the number of days between observations of individual animals is presented in Table 2-19. Qualitatively, there appeared to be little difference in the distance moved per day by individuals between years. One 12 year old male, handled in 1984 and 1985, had a weighted mean distance moved per day of 0.4 km/day in both years. This bear was resighted on the same spit of land four times over 35 days in 1984, and five times over 30 days in 1985. There was no apparent trend for individuals that moved greater or lesser distances per day in one year to follow a similar pattern in another year. In general, the weighted means were within one standard error between years and between most individuals.

2.3.3 Direction of movement

The direction of movement between each successive location of a bear was determined for all movements greater than two kilometers. Almost seven hundred bearings were analyzed for the five classes of bears over the length of the study period. Insufficient information precluded the analysis of orientation patterns during July for all groups except adult males. As many animals were resighted within two kilometers of their previous location, the information on orientation does not necessarily imply a shift

in the population, but does indicate the mean direction of migration in bears that were moving. The mean vector of orientation (r) represents a composite of many small scale movements over the relocation intervals and over many years. For this reason, detailed aspects of movement patterns and orientation are obscured.

Family groups illustrated significant orientation during August and October with mean headings of 196° (r=0.44; n=21; P=0.015) and 30° (r=0.42; n=48; P<0.001), respectively (Figure 2-9). No significant orientation was found during September and November. The percentage of the relocations less than two kilometers apart were 19 (5/26), 21 (6/29), 14 (8/56), and 23 (3/13) for August through November, respectively.

Lone adult females had a significant (P<0.001) orientation of 169° (r=0.70; n=15) during August (Figure 2-10). A significant (P<0.001) bimodal axis of orientation of 339° (r=0.92; n=12) was found during September. No significant orientation was observed during October and November. The percentage of bears not moving more than two kilometers between relocations were 17 (3/18), 20 (3/15), 34 (16/47), and 36 (5/14) for August through November, respectively.

Subadult females showed no significant orientation during August and September, but did show a significant mean bearing of 324° (r=0.30; n=41; P=0.026) and 340° (r=0.32; n=28; P=0.046) for October and November, respectively (Figure 2-11). Only during October and November were subadult females resighted within two kilometers of their previous location. In 1984 and 1985, only 4 percent (1/24) of consecutive sightings fell into this class during October and November. For all years combined the values were 49 (39/80) and 20 (7/35) percent for October and November, respectively. These higher values are influenced by studies at Cape Churchill in which bears could only be observed in the area nearby.

Adult males showed a significant orientation in their movements during August, October, and November with mean bearings of 166° (r=0.45; n=111; P<0.001), 352° (r=0.41; n=103; P<0.001), and 329° (r=0.41; n=22; P=0.027), respectively (Figure

2-12). A bimodal axis of orientation was found during September with a bearing of 348° (r=0.48; n=63; P<0.001). Movements roughly perpendicular to the mean bearings were common from August through November and appeared to be caused by movements into and out of areas further inland. The general trend for adult males appears to be movement parallel to the coast in all months. The percentage of adult males not moving more than two kilometers between successive relocations were 33 (4/12), 30 (47/158), 34 (33/96), 22 (29/132), and 19 (5/27) for July through November, respectively.

Only during October, subadult males as a group showed a significant non-random orientation with a mean heading of 328° (r=0.29; n=40; P=0.034) (Figure 2-13). Movements of less than two kilometers accounted for 11 (2/18), 15 (2/13), 31 (18/58), and 15 (5/34) percent of the observations for August through November, respectively. These are probably slight overestimates of the population as a whole due to biases associated with studies at Cape Churchill. Only 11 percent (3/28) of all consecutive sightings were within 2 km during October and November, 1984 and 1985.

2.3.4 General fidelity to the study area

General fidelity to the study area was described by using the ratio of the number of bears tagged in the study area to the total sample of bears in both capture programs and hunter tag returns from various locations about Hudson Bay (Table 2-20). While information from eastern Hudson Bay is limited and the total harvest unrecorded, few bears tagged in the study area are reported from this area. The degree of reporting of tagged bears from the Northwest Territories and Ontario appears to be fairly complete (J. Lee, G. Kolenosky personal communication). A confounding factor in the analysis of hunter kill information is the unidirectional information that it yields on site fidelity. While it provides an estimate of emigration and dispersal patterns, it does not permit the subsequent return of animals back to the study area. For this reason it is impossible to determine if a recorded kill location represents a dispersal movement or if the kill site is

part of regular seasonal movement patterns. However, the ratio does present an index of movement and fidelity in a broad context. There was a general trend for the proportion of bears tagged within the study area to decrease in samples as the distance from the study area increased. A major change in the proportion of tagged bears appears to occur between Rankin Inlet and Chesterfield Inlet to the north and between the mouth of the Nelson River and the Manitoba-Ontario border to the south. The harvest of polar bears along the western coast of Hudson Bay is composed of 38 percent subadult males, 28 percent adult males, 20 percent subadult females, 12 percent adult females, and 2 percent unrecorded (n=424). Within the harvest, 37 percent (38/102) of the tagged bears taken between Eskimo Point and Rankin Inlet were known to be within the study area in the previous six months.

Of the 7 tag returns from Quebec, 5 were males with a mean age of 3.4 years (S.E.=0.5, n=5). The remaining 2 bears were adult females aged 6 and 19 years. The mean interval between the last known location of the bears within the study area and the date of harvest was approximately 13 months (S.E.=5.0; n=7), although 4 were killed within five months of their last sighting in the study area. Movements from the study area to the coast near Inoucdjouac, Quebec, where most of the recorded harvest is centred, represents a straight line distance of approximately 900 km. The single tagged bear killed in the Belcher Islands was a 5 year old male that had moved over 800 km in the four months since it was last handled at Cape Churchill, Manitoba.

Studies by the Ontario Ministry of Natural Resources (OMNR) have resulted in a total of 450 polar bear captures between 1984 and 1986 in Ontario. Of this sample, only 6 percent (28/450) had previously been handled within the study area in Manitoba. The 28 recaptures represent 23 different bears, previously handled in Manitoba, of which 15 were males. Three of the recaptured bears in the Ontario study were handled in two different years and one adult male was handled in all three years. Three of the 23 bears were members of the same family group, first handled as the female with two

cubs-of-the-year left the maternity den, but captured independently in Ontario. The mean age of recaptures in Ontario was 10.7 years (S.E.=1.7; n=10) and 10.8 years S.E.=1.4; n=18) for females and males, respectively. The mean age of the recaptured bears, when last handled in Manitoba, was 7.5 years (S.E.=1.9; n=8) and 9.3 years (S.E.=1.6; n=15) for females and males, respectively. Of the 23 recaptured bears, 8 males and 3 females were 5 years of age or younger when last captured in Manitoba. One female, first handled in the study area as a three-month-old cub-of-the-year in March 1982, was captured by OMNR 273 km to the east-south-east in 1984. This same bear was later recaptured in September 1986 within 17 km of her natal site. Her weight (205 kilograms) and general appearance indicated that she may have been pregnant.

The mean distance between the positions of females and males caught in the study area and in Ontario was 328 km (S.E.=8; n=41) and 321 km (S.E.=7; n=80), respectively. None of the bears captured in Ontario, previously captured in Manitoba, were more than 94 km from the Manitoba-Ontario border (G. Kolenosky personal communication).

From 1967 to 1975, 73 bears were caught along the Ontario coast and James Bay and only one bear has been caught within the study area. The bear, a two-year-old male when first captured at Cape Henrietta Maria (northwest corner of James Bay) in 1968, was recaptured in 1984 and 1985, having moved over 750 km from the initial capture location. A recent and ongoing study by the Northwest Territories Wildlife Service (NWTWS) in the area of Southampton Island and Wager Bay (west of Southampton Island) has resulted in 119 captures. None of the bears had been handled in the study area and none of the bears from the NWTWS study have been found in Manitoba. During 1974-1979, a total of 231 polar bears were captured in the southeast Baffin Island area. None of these bears have ever been captured in Manitoba.

The area to the immediate southeast of the study area has received little active research in recent years other than periodic capture sessions by OMNR and CWS. In

general, few bears are seen in this area. Of the 39 captures in the area from the mouth of the Nelson River to the Manitoba-Ontario border, only 8 bears had been handled previously in the study area. The ages of recaptured females were 2, 16, and 20 years. Recaptured males were 2, 3, 9, 9, and 17 years.

2.3.5 Fidelity within the study area

Similar relocation distances were found between sexes and across age classes. The data may be biased as bears that did not return to the study area are not included in the sample. Distances between relocations do not necessarily represent minimum values as individuals may have moved closer to previous positions, but were not seen. Relocation intervals did not change significantly when harvest information was removed.

Adult females were relocated a mean distance of 32.9 km (S.E.=3.3; n=129) between known positions with a relocation interval of 3.3 years (S.E.=0.3; n=129) based on 37 different bears (Figure 2-14). The contribution of each month was 13, 6, 48, and 33 percent for August through November, respectively. No harvested bears were used in this analysis. Females handled as subadults and later as adults were found an average of 31.6 km (S.E.=4.4; n=103) between positions (Figure 2-14). This was based on 26 different bears with a relocation interval of 6.8 years (S.E.=0.4; n=102). Harvest information did not meet the criterion of the analysis for this group and were not included. Based on a sample of 26 different subadult female bears, relocated as subadults, the mean distance between known positions was 42.1 km (S.E.=9.3; n=50) (Figure 2-14). The mean relocation interval was 1.3 years (S.E.=0.5; n=50) with a monthly contribution of 10, 4, 56, and 30 percent of the sample from August through November, respectively. Without harvest information the mean relocation distance drops to 29.7 km (S.E.=6.4; n=47) and is based on a sample of 23 individual bears.

Adult males relocated in subsequent years were found a mean distance of 35.3 km (S.E.=3.7; n=276) between positions (Figure 2-15). This was based on a sample

of 50 different bears with a relocation interval of 1.8 years (S.E.=0.1; n=276). The contribution of each month was 31, 24, 36, and 9 percent for August through November, respectively. Only three harvested adult males were included in the analysis, but when removed the relocation distance dropped to a mean of 32.4 km (S.E.=3.1; n=273). The mean relocation distance between the positions of subadult males and their known locations as adult males was 41.5 km (S.E.=7.44 n=123) with a mean interval of 3.9 years (S.E.=0.3; n=123) (Figure 2-15). This was based on 38 different bears with 2, 74, and 24 percent of the information from September, October, and November, respectively. Removal of harvest information dropped the mean relocation distance to 23.0 km (S.E.=3.2; n=115) and is based on 34 bears. Subadult males relocated as subadult males were found an average of 25.3 km (S.E.=4.3; n=102) between positions at an interval of 1.3 years (S.E.=0.1; n=102) (Figure 2-15). This was based on a sample of 46 different bears with a monthly contribution of 3, 2, 55, and 40 percent for August to November, respectively. Subadult males compose a large portion of the harvest in western Hudson Bay and when this information is removed the relocation interval drops to a mean of 16.2 km (S.E.=2.4; n=96) and is based on a sample of 44 bears.

The mean distance between known positions of cubs-of-the-year and yearlings with their mothers and their locations as independent subadults and adults was 52.7 km (S.E.=6.4; n=163) (Figure 2-16). This was based on 60 different bears, of both sexes, and was across all months, with a mean relocation interval of 4.4 years (S.E.=0.4; n=163). Without harvest information the relocation distance drops to 34.7 km (S.E.=3.6; n=150) and is based on 53 bears.

2.3.6 Single ice-free season fidelity

During 1984 and 1985, an effort was made to search outside the study area in order to assess the degree of emigration during the study period. Of 200 independent

bears captured within the study area during the fall of 1984 and 1985, only two were known to have moved outside of the study area before freeze-up. One three-year-old male moved 94 km to the northwest and the second, a 19 year old male, moved 156 km to the southeast.

Of the independent bears handled during 1984 and 1985, 86 percent (172/200) were resighted at least once within the study area after capture. Based on radio tracking data at least 96 percent (85/89) of the bears handled remained within the study area until freeze-up. No radio tagged bears were known to have moved out of the study area, although four bears were not relocated or seen after release. In 1984, the two radio tagged bears not relocated were both two-year-olds with eartag radios; one was a female and the other a male. During 1985, two radio collared adult females, one 17 years old with two cubs-of-the-year and the other a solitary 8 year old, were not relocated during tracking surveys. It is possible that the radios had failed. The missing or potentially emigrating bears in the population were not dominated by any single age, sex, or reproductive class.

The degree of immigration into the study area is difficult to assess as few animals were marked along the periphery. During 1984 and 1985, only three animals, of over four hundred bears handled during the ice-free period in Ontario and eastern Manitoba by the OMNR, were known to have moved into the study area. None of the 119 bears handled in the Southampton Island area by the NWTWS were found within the study area.

2.3.7 Winter distribution

A total of nine bears were located on the sea ice during the winter radio tracking survey of March 1985, one of which was radio tagged, in Ontario, by the OMNR. Seven of the nine bears were adult females, one a subadult female, and one an adult male. The locations of an adult female, a subadult female, a subadult male, and an

adult male were obtained in February 1986 during an OMNR survey. Figure 2-17 shows the sea ice positions of known polar bears, that were handled within the study area. In 1985 and 1986, the mean distance between the last known position of bears on land in the study area and their location on the sea ice was 195 km (S.E.=23; n=12). The bear handled in Ontario had moved 347 km from its last known location. A significant (P=0.002) non-random orientation of 53° (r=0.68; n=12) was observed in the movements of bears from the study area to the locations found on the sea ice. Some additional late fall radio locations and spring captures are included in Figure 2-17. The late fall positions demonstrate the tendency for some bears to travel north along the newly formed sea ice as it rims the coast.

The ice in the area surveyed appeared to be moderately active and was interspersed with numerous open and refrozen lead systems up to at least 370 km offshore. Several ringed seals were seen when flying at low elevations in the region where most of the radio tagged bears were found. In this same area, five unmarked bears were seen, including one unidentified adult male feeding on a ringed seal.

2.3.8 Testosterone levels in adult males

Blood serum testosterone levels were analysed from some of the the bears that were handled in an attempt to determine the influence that it may have upon the distribution patterns seen in adult males. Samples were available from studies in the Beaufort Sea which were collected during the breeding season (April-May). This allowed a comparison of testosterone levels between bears captured during the breeding season and those handled during the ice-free period in western Hudson Bay.

There was a significant difference (Mann-Whitney U=906.0; P<0.001) between the testosterone levels of bears captured in the spring ($\bar{X}$=7.48 ng/ml; S.E.=0.94; n=38) and those captured during the fall ($\bar{X}$=1.03 ng/ml; S.E.=0.17; n=26). An analysis to determine if blood serum testosterone levels were different between adult

males along the coast and those using inland areas revealed no significant differences (t_{24}=0.37; P=0.717). Males along the coast had a mean testosterone level of 1.07 ng/ml (S.E.=0.20; n=19) and males inland had a mean of 0.93 ng/ml (S.E.=0.37; n=7).

2.3.9 On land feeding

During capture activities in September 1986, I collected scat samples from 15 bears and gather associated information on the feeding habits of polar bears in the inland area. No statistical analyses were performed because sample sizes were small.

The major components found in the scats were: *Vaccinium uliginosum, Empetrum nigrum*, various grasses and sedges, mosses, and feathers (Table 2-21). Trace amounts of *Kalmia polifolia, Betula glandulosa, V. vitis-idaea*, lichens, arthropods, polar bear hair, and sand were found in many scats and was recorded in the miscellaneous category. Many of these trace items may have been ingested passively during foraging or grooming. Three scats contained feathers that were believed to be from Canada geese (*Branta canadensis*), although an absence of hard tissues precluded confirmation.

Twenty-one percent (21/99) of the independent bears handled in 1986 showed some evidence of feeding (*eg.* defecated while handled). It was not possible to determine the importance of feeding at this time of the year or to assess the amount of time devoted to this activity. Two of seven suspected pregnant females handled in 1986 were found to be feeding; one largely on *V. uliginosum* and the other predominantly on moss. There appeared to be some differences in the scat composition of adult females and subadults in the inland areas when compared to adult males and subadults along the coast, although a larger sample would be necessary to test this. Adult females and subadults appeared to be foraging more on *V. uliginosum* than adult males.

Bears along the coast and inland have shown signs of feeding during capture sessions in July and Augusts in previous years, but in general feeding appeared less

prevalent earlier in the ice-free period. Scavenging on ringed seals, white whales (*Delphinapterus leucas*), polar bear, and caribou (*Rangifer tarandus*) carcasses was observed during the 1984 and 1985 ice-free periods. It was not known whether or not the bear feeding on the bull caribou carcass had killed the animal or was scavenging. Two adult males were observed feeding on seals, that they had presumably killed, during early November at the edge of the newly formed sea ice.

Bears were observed feeding on polar bear carcasses three times between 1984 and 1986. Two of the bears had been killed by humans and the cause of death of the third, a yearling, was unknown. The mother and sibling of the yearling were seen resting next to the partially consumed carcass.

2.4 Discussion

The distribution and movement patterns of polar bears within the study area varied according to the age, sex, and reproductive status of an individual. Philopatry was demonstrated by all age and sex classes.

Handling of the bears is potentially the greatest bias affecting the observed patterns of movement and distribution. Ramsay and Stirling (1986b) reported that drugging and handling of polar bears may have a slight negative long-term effect on adult females with cubs as recaptured females tended to have smaller litters and lighter cubs. They also reported that 10 of 13 pregnant females handled in October or November abandoned dens and moved a median distance of 24.5 km. These effects, while important, probably do not directly affect or significantly influence the results of this study. Ramsay and Stirling (1986b) concluded, that while the biological significance of handling was unknown, it did not appear to disturb polar bears sufficiently to severely bias data. The general similarity between the data collected from radio tagged bears in 1984 and 1985 and all other captures and sightings from 1966 to 1985 indicate that, despite possible biases, the polar bears in the study area show distinct and recurrent distribution patterns. Given the relatively small number of bears with radios, it was not possible to compare all aspects of the study for bias, but I felt that the resulting patterns were a function of real differences in the behaviour of different groups.

2.4.1 Family groups

A general trend for adult females to move into the inland areas was evident for much of the ice-free period and family groups were significantly separated from most adult males from August through November. Avoidance of conspecifics has been forwarded as a possible mechanism through which polar bears disperse themselves throughout an area (Latour 1981a). Kolenosky and Prevett (1983) noted that the distribution of family groups differed from that of other age and sex classes and believed

that the attendant risk of predation of young by adult males was responsible. Intraspecific aggression and cannibalism has been observed in polar bears and attacks by adult males on small cubs or subordinate animals may influence distribution patterns (Jonkel 1970; Lunn and Stenhouse 1985; Taylor *et al.* 1985). Russell (1971) observed an adult male feeding on an adult female and two cubs-of-the-year in August shortly after the family had come off the sea ice. Russell believed that the male had killed the family, but had not observed the incident. Social interactions have been proposed as a mechanism of population regulation in black and grizzly bears by influencing emigration patterns and through cannibalism (Beecham 1980; Young and Ruff 1982; McCullough 1981; Stringham 1983; Tietje *et al.* 1986). Stirling (1974) indicated that adult males do not necessarily dominate females with cubs and that given that older cubs can outrun adult males, the occurrence of intraspecific predation is incidental.

During the ice-free period of 1984, 3 of 36 cubs handled died independent of handling activities. Two of the deaths occurred along the coastal region and the other cub disappeared in the inland area. A yearling was found dead and partially consumed near a large concentration of bears and a cub-of-the-year was seen dead, near its mother, in an area of low bear density along the southern coast. The cub-of-the-year missing in the inland area was in poor condition at capture and had a large wound on its back. The actual causes of mortality of all three cubs were unknown and may have been the result of causes other than infanticide. Ramsay and Stirling (1984) documented that wolves (*Canis lupus*) periodically attack and kill young polar bear cubs during the spring, but by the fall the size and mobility of the cubs is such that predation by wolves is unlikely.

Females with cubs may perceive adult males as a threat to their offspring even after cubs are large enough to evade adult males (Taylor *et al.* 1985). Observations that cubs are extremely nervous in meetings with any unrelated bear (Stirling 1974; Latour 1981a; Lunn 1985) may indicate that the general avoidance of conspecifics could have a

strong adaptive value. Given the low reproductive potential of female polar bears and the substantial investment represented in each cub, the loss of offspring during the fall may seriously affect the overall reproductive output of a female. Lunn (1986) noted that females with cubs were the most aggressive bears at a dump situation, but also recorded that family groups do interact non-aggressively with each other. Observations of females with young cubs-of-the-year in close association with other family groups in high density maternity areas have also been recorded (Hansson and Thomassen 1983). It appears that adult females with cubs may avoid lone bears, but may be more tolerant of other family groups. This is consistent with the findings of this study where several family groups were often found in close proximity (*eg.* within 500 meters).

Latour (1981a) reported that segregation appeared to be density dependent and that most of an individual's social behaviour is directed at members of the same age and sex group. Intraspecific aggression does not adequately explain all of the dynamics of the spatial and temporal distribution of family groups. Several adult males were found in the inland areas, often relatively close to family groups, and conversely family groups were found along the coast throughout the ice-free period. If the distribution of adult females with cubs was only a function of the threat of cannibalism then the optimum strategy of all females should be to move inland to such a distance that the chance of encountering an adult male is minimal. An alternative to moving inland could be to use other areas where bear densities are extremely low, such as the region north of the study area. The absence of family groups and other bears in areas north of Churchill indicates that factors other than intraspecific aggression are functioning.

Differences in the distribution of adult males and adult females with cubs-of-the-year have been found for polar bears on the sea ice in the Beaufort Sea (Stirling *et al.* 1981). Adult females with yearling and two-year-old cubs were found to frequent both the ice types used by adult males, presumably for the higher availability of ringed seals, and those used by females with younger cubs (Stirling *et al.* 1981).

Females with cubs-of-the-year avoided the areas used by adult males, probably because of the threat of infanticide and potential hypothermia in small cubs if they have to swim in open water prevalent in habitat used by adult males (Stirling *et al.* 1981). If females with yearlings in the study area are less susceptible to intraspecific predation, and energy conservation by reduced movement is a strategy during the ice-free period, then they might be expected to utilize areas used by adult males more often than females with cubs-of-the-year. However, that was not found. The lack of overlap in the areas used by adult females with yearlings and adult males may be explained by two hypotheses. First, family groups may be selecting habitat based on factors other than intraspecific predation or alternatively, that the returns for utilizing the habitat of adult males are insufficient to overcome any potential negative returns. This contrasts with the situation on the sea ice in winter when greater access to food resources may be important. The high density of bears in western Hudson Bay during the ice-free periods may alter the dynamics of distribution as the potential of encountering conspecifics may be higher than on the sea ice. Family groups may move into the inland areas due to the lower bear density and subsequent reduced probability of being harassed. This would reduce avoidance behaviour and confrontations that are energetically expensive and possibly life threatening.

The distribution of adult females with cubs may be influenced by the age and weight of individual females. The distance from the coast had a weak negative correlation with weight and indicated that some lighter females moved further inland than heavier females during August through October. This may be due to the higher energetic cost of movement for heavier adult females and the greater risk of hyperthermia during warm periods. Polar bears have been reported to be locomotively inefficient (Hurst *et al.* 1982a,b; Best 1982) and are subject to hyperthermia when traveling under warm ambient temperatures as they are unable to dissipate sufficient body heat (Øritsland 1970; Best 1982). During October and November, the tendency for

older females to remain inland may be a function of learning the cues that indicate the timing of the formation of the sea ice. Alternatively, the return to the coast may be related to avoiding adult males and waiting until they have moved onto the sea-ice, the timing of which may be learned over several years. Anecdotal observations from Cape Churchill indicate that family groups continue to arrive at the coast after most other bears have returned to the sea ice.

Adult females with cubs were distributed further inland than were subadult females and subadult males from September through November and August through November, respectively. If family groups are actively seeking areas of low bear density then the avoidance of areas closer to the coast, where subadults are found, may function to separate the groups. Alternatively, segregation of families and subadults may be a function of avoidance behaviour by subadults as adult females with cubs are more aggressive (Lunn 1986). However, as with comparisons between all groups it is impossible to determine which group is actively selecting a habitat, which are passively distributed about the area, and which are being displaced from preferred areas, given that they exist. The differences in the distribution of family groups and lone adult females is probably not a function of avoidance by family groups, but may be the result of the habitat selection by pregnant females and their avoidance of other bears.

Family groups were relatively close to the coast in July, as they arrived off the sea ice, and subsequently moved into the inland areas during August, September, and October, and returned to the coast during November. The heading that family groups took as they moved from the coast inland was variable, but on average it was approximately 180° to the orientation of 39° (r=0.94; n=64) that Ramsay and Andriashek (1986) found for bears leaving the denning area in the spring. Families moving to the northwest were generally those that were captured in the southern part of the study area, while those moving southward were caught in the northern areas. The general trend for all families to move into the inland areas seemed independent of their

position along the coast. The lack of significant orientation in family groups during September coincided with reduced levels of activity. As family groups moved out of the inland area they showed a significant non-random orientation similar to the orientation found by bears during the spring by Ramsay and Andriashek (1986). The higher degree of variability in the direction back to the coast in fall is probably a function of three factors. First, the snow during spring allows the bear's exact path to be followed, while the fall data represent only a general pattern of movement based on periodic relocation intervals. The second factor may be related to the poor condition of the females in the spring, which after a long period without access to high energy food and the energetic costs of lactation, may need to return to the sea ice as directly as possible. The final factor may be that some adult females with cubs use the Churchill dump during the fall and orientate themselves to reach it. Ramsay and Andriashek (1986) speculated that the orientation pattern that they observed may have been a function of the bears moving to an area of active sea ice with good hunting identified by Stirling *et al.* (1977). The information collected during this study confirmed that the area to the northeast of Cape Churchill is used by bears from the study area for hunting. Females with cubs move to the coast and towards the areas where they may gain earlier access to the sea ice and food.

The analysis of distance moved per day showed a general pattern of decreased movement during September. This may be a function of energy conservation by females with cubs by moving to preferred areas during July and August followed by reduced activity until the sea ice starts to form in late October and early November. Lunn and Stirling (1985) suggested that polar bears during the ice-free period remained inactive in order to reduce energy utilization and the risk of hyperthermia. This appears consistent with the observation that between 19 and 23 percent of consecutive sightings were less than two kilometers apart. Problems associated with hyperthermia are only a factor in the earlier part of the ice-free period when temperatures are higher. The significant

correlation between weight and distance moved per day during October may be a function of lighter females becoming nutritionally stressed and subsequently moving more to locate food sources. This correlates with the findings of Lunn and Stirling (1985) which found that bears began to move into the dump during October.

Adult females in general show fidelity to the study area and females captured in the spring leaving the denning area show a strong tendency to return to the study area for the ice-free period. The fidelity of adult females with cubs may function to familiarize female cubs with habitats suitable for denning. Young female grizzly and black bears often show a predilection to remain on the maternal home range and to subsequently include it, or portions thereof, in their adult home range (Pearson 1975; Jonkel and Cowan 1971; Glenn and Miller 1980). Polar bears in western Hudson Bay move much greater distances between denning areas and feeding and breeding habitat than do either black or grizzly bears, but preliminary indications are that some of the females born in the area return to den. Hansson and Thomassen (1983) found that polar bear cubs on average only spend two weeks near their maternal den before leaving for the sea ice. This may allow sufficient time for cubs to learn the general position of their den, but there may be adaptive benefits for an adult female to return to the denning area with her cubs to reinforce the areas and travel routes taken between the breeding and hunting areas and the denning area. Three members of the same family group, first captured in Manitoba, subsequently recaptured independently in Ontario, may indicate that maternal movement patterns are passed onto offspring. The adult female was caught in Ontario in 1985 and 1986. It seems probable that the movement patterns of the independent offspring were influenced by the areas traversed when with their mother. Family groups in higher latitude populations have also been observed during the summer in areas used for maternal denning (I. Stirling personal communication). Schweinsburg (1979) reported the use of summer snow dens by family groups and other bears in the northern Baffin Island area, but was unable to determine the function of

them. This same region has been reported as a maternity denning area (Schweinsburg *et al.* 1982).

Most adult females with cubs-of-the-year appear to be lactating throughout the ice-free period and therefore are experiencing a substantial draw on their stored fat and mineral reserves. Lunn (1985) reported a mean weight loss of 34 kilograms between the summer and fall period for adult females with cubs that did not use the dump. Given the high energy demands on adult females with cubs, they may be expected to use available energy sources such as the Churchill dump. Polar bears have been reported to feed sparingly while on land and the energetic returns have been thought to be low (Russell 1975; Knudsen 1978; Lunn and Stirling 1985). The collection of scats in the inland area indicated that some bears were selectively foraging on *V. uliginosum* berries. Russell (1971) thought that polar bears in the inland areas were feeding on *Vaccinium* spp. and *E. nigrum*, but was unable to document their importance. The relative importance of feeding during the onland period is difficult to quantify, but Bunnell and Hamilton (1983) found that *V. corymbosum* was highly digestible by grizzly bears. Kurten (1964) noted that fossil remains of polar bears date back only 70,000 years before present, evolving from a grizzly bear ancestry, and noted that polar bears may still have digestive capabilities similar to grizzly bears.

V. uliginosum is widely distributed throughout the inland area and is commonly found on the summits and upper slopes of ridges (Ritchie 1960) and is associated with both dry and moist acidic soils (Porsild and Cody 1980). Lunn (1985) concluded that polar bears in the inland areas of the study area were not feeding, but his use of urea to creatine ratios to test this may not be sensitive enough to detect a predominantly carbohydrate diet (R. Nelson personal communication). Low crude protein contents of 3 to 6 percent by dry weight have been reported by Eagle and Pelton (1983) and by Landers *et al.* (1979) for other *Vaccinium* species. Observations of the importance of food to polar bears during the ice-free period have been biased by sampling in areas and

at times when foraging on berries would not be high. Knudsen (1978) was biased in his observations of activity in polar bears to the midday period, the warmest part of the day, and Russell (1975) was biased towards the coastal areas dominated by adult males and away from potentially desirable forage species.

In addition to the energetic benefits from foraging on *V. uliginosum*, the acquisition of minerals and vitamins may be important. Landers *et al.* (1979) reported a calcium content of 0.13 percent by dry weight in *V. stamineum* berries which may be important to lactating females. Milk samples collected during the ice-free period have a strong plant-like odour, unlike specimens collected while bears are feeding on seals. It is difficult to determine the importance of summer and fall foraging to family groups. Given the potentially high energy return to a female and her cubs, foraging may aid substantially in their energy budget and may act to reduce the rate of weight loss. Different nutritional requirements of male and female red deer (*Cervus elaphus*) have been thought to be the cause of spatial segregation of sexes outside of the breeding season (Watson and Staines 1978). Berries in the inland area may represent a predictable high quality food source and while it is unlikely that their presence is the sole reason for family groups to move inland, it may be an additional benefit.

Another factor that may influence the distribution of family groups is the occurrence of permafrost in the inland area which bears sometimes exposed by digging shallow pits and dens for use as beds. Pits and dens are thought to serve a thermoregulatory function through access to the permafrost layer and the avoidance of direct sunlight (Jonkel *et al.* 1972). Dens may also serve as protective cover, but families use them infrequently. Dens may also be used to avoid biting insects that are abundant during the summer.

2.4.2 Lone adult females

The distribution and movement patterns of lone adult females resulted in a high degree of separation between this group and adult males and subadults from September through November and additionally from adult males in August and families in October. The factors associated with the segregation of solitary females are different than those influencing adult females accompanied by cubs.

Most of the lone adult females in the study area are pregnant and this is a major factor influencing their distribution and movement patterns. Also included in this group are non-pregnant females that may compose from 17 percent of the group based on blood serum progesterone levels (Ramsay 1986) to 22 percent based on movement patterns and distribution information. Some evidence of reproductive senescence in female polar bears has been reported (Stirling *et al.* 1984; Ramsay 1986) and these animals were also included in the lone adult female group, as were females that may have lost or weaned cubs and did not breed.

Lone adult females move inland soon after they arrive off the sea ice. The proportion of the sightings of this group less than two kilometers between sightings increased from August through November and the median distance moved per day decreased, indicative of pregnant females finding suitable denning sites. Pregnant females select denning locations in areas isolated from most other bears. However, there appears to be a general tolerance of other females denning nearby and active dens have been found within 100 meters of each other. Up to 9 dens in an area of one tenth of a square kilometer have been recorded in Svalbard during the spring and no overt signs of aggression between females were seen (Hansson and Thomassen 1983).

The segregation of solitary females from most of the population may be a function of habitat selection rather than active avoidance of conspecifics. The distribution of dens in the study area, ranging from approximately 10 to 100 km from the coast, has been described by Stirling *et al.* (1977) and Ramsay (1986). Kolenosky

and Prevett (1983) reported that maternity dens in Ontario were found an average of 61 km from the coast along lake and creek banks with sufficient peat deposits.

Movements patterns of pregnant females are influenced by fidelity to given areas, but the importance of fidelity is difficult to quantify. Based on limited data, Ramsay (1986) reported a mean distance of 27 km between the den sites of individual females captured at dens in different years and concluded that pregnant females show little fidelity to specific sites, but do return to the same general area. Finding an appropriate location to den appears to be based on factors other than previous denning sites. This may be influenced by the widespread distribution of suitable habitat, although some lakes and creeks are used repeatedly and the distribution of dens is somewhat clumped (Stirling *et al.* 1977; Ramsay 1986). There may be no net benefit to a female to show fidelity to a den that she has used before, if suitable habitat is abundant, but the benefits of returning to a general area that in the past has provided good habitat are probably greater than looking for new areas. The prevalence of slumping of older dens sites may be a factor in females not returning to the same den. Small excavations along lake and creek banks, movement patterns, and direct observations indicate that pregnant females may test several potential den sites for their suitability prior to selecting a maternity site. The factors involved in the selection of a den site are not well understood and therefore the distribution and availability of suitable habitat is unknown. Selection of sites under clumps of spruce was common and is likely related to the added support that the roots give to the peat and the greater snow accumulation that is important in the winter when the bears move into snow dens. Inland movement is probably constrained by the presence of continuous coniferous forest, where deep unconsolidated snow accumulates, which is unsuitable for digging dens and difficult for females with young to travel through during the spring.

The orientation of lone adult females moving into the denning area is difficult to assess as they generally exhibit a brief residency along the coast and few were captured

there. A significant orientation was found during August, roughly parallel to the coast, but is biased due to the greater sampling and visibility of bears in the coastal area while capture operations were in progress. Of the 11 bears in the August sample, 8 were moving along the coast. Little information was available for bears further inland. Some of the females along the coast were pregnant. One particularly obese female (492 kg at capture) moved 61 km along the coast until late September when she moved into the denning area. The movements of this bear may have been influenced by her extremely high weight and the associated high energetic costs of movement confounded by the problems of thermoregulation and hyperthermia. Her exact den site was not determined, but appeared to be approximately 12 km from the coast and she was known to have successfully produced triplets. The bimodal axis of orientation found during September is difficult ~~to explain as~~ 8 of the 11 females were in the inland area, over 20 km from the coast. It is possible that females are moving or navigating by using landmarks (review by Able 1980) such as beach ridges and major lakes that parallel the coast. The lack of orientation during October and November is possibly due to the searching for den sites by some pregnant females and the movements of the more active non-pregnant females.

The weight of a solitary adult female did not appear to influence the distribution of individuals during August and September. During October and November, a significant trend for heavier females to be found further inland can be attributed to the movement of lighter animals back towards the coast. An examination of the solitary females outside of the normal denning area revealed that they were an average of 51 kg and 67 kg lighter than females in the denning area during October and November, respectively. Ramsay (1986) reported that known pregnant females in the fall had a mean weight of 234 kg, approximately 75 kg heavier than females with cubs-of-the-year ($\bar{X}$=159 kg) when they emerged from dens in the spring. The mean spring weight of adult females with cubs-of-the-year is similar to that found for the solitary females

along the coast in October and November. It seems plausible that the solitary females that leave the denning area or never enter it were not pregnant or failed to store sufficient body reserves to maintain body functions, produce and nurse cubs, and return to the sea ice. Rogers (1976) proposed that female black bears with insufficient body reserves may fail to implant the blastocyst and forgo reproduction that year. Pregnant females with lower body weight may receive hormonal cues associated with denning behaviour, but later in the fall, if blastocyst implantation is not achieved, a different series of cues may occur that results in movement back to the coast.

The negative correlation of age with the distance moved per day during September may be a function of younger females searching greater areas for suitable den sites and the movements of young non-pregnant females. Kolenosky and Prevett (1983) thought pregnant bears in Ontario moved inland during late September to early November, although they admitted the absence of good documentation. All seven of the lone adult females handled during September 1986 were in dens. The similarity between the Manitoba and Ontario areas makes it unlikely that the populations differ with respect to the timing of movement inland.

Pregnant polar bears in the study area demonstrated reduced movements through the ice-free period and were not usually seen outside of the den beyond early October. Bears that were sighted were lying beside their den or nearby. Black and grizzly bears demonstrate a pre-denning lethargy (Beecham *et al.* 1983; Craighead and Craighead 1972) that may be similar to the movement patterns of pregnant polar bears.

Two of seven suspected pregnant bears handled in September 1986 had been actively foraging. It was not possible to determine the importance of fall foraging by pregnant females, but it may assist them in their overall energy balance. Given the long period between the availability of seals to pregnant females, it seems likely that they would make use of a high quality resource if energetically efficient to do so.

The factors that determine the movement patterns and the distance inland that a female moves prior to the selection of a den site are unknown. There is an energetic cost of moving far inland to den both in the fall and in the spring as the females move back to the sea ice with young cubs. In polar bear populations at higher latitudes most pregnant females den within a few kilometers of the coast (Harington 1968; Stirling *et al.* 1975). Larsen (1985) found most maternity dens within 3 km of the coast in Svalbard. The benefits, if existent, of moving 90 km inland when denning habitat begins within 15 km of the coast, are unclear. Better denning habitat, reduced levels of interaction with other bears, and learned behaviour may be involved. The added energetic costs of denning inland may not be critical to the energy budget of the bears and might be outweighed by the benefits.

2.4.3 Subadult females

The distribution and movement patterns of subadult females and the factors influencing them are not as apparent as those for older females. Subadult females, like all other bears on land during the ice-free period, are constrained to some degree by their stored fat deposits to carry them through the fall until they return to the sea ice. The conservation of these energy stores is crucial to their survival. Unlike older animals, subadults are further burdened with the energy demands of growth. A second factor influencing the movements and distribution of subadults is their relatively low position in the dominance hierarchy and subsequent displacement by higher ranking individuals.

Most subadult females occupy different areas than family groups and lone adult females from September to November. This segregation appears to be a function of factors that move adult females further inland. Given that the areas used by all females overlap during July and August and the segregation coincides with the inland movement of adult females, it is unlikely that intraspecific aggression functions to segregate the groups later in the fall.

The factors influencing the different areas used by subadult females and adult males during August are difficult to determine, but subadult females may select habitat with lower densities of adult males in order to reduce the likelihood of interactions. This behaviour may be learned from the time spent with their mothers or from periods on the sea ice when interactions with adult males are liable to be detrimental. If subadult females are actively avoiding adult males, it is most likely important during resting periods. If subadults were awake, their greater speed and agility would make them unlikely prey for adult males. Subadult females were often seen in close proximity to adult males and if the attendant risk of predation was substantial then the occurrence of the association should be rare. Comparisons made with only those animals with radios indicated that the areas used by the two groups showed substantial overlap in all months.

The variation in the behaviour of individuals is substantial and is probably influenced by past experience and patterns learned from their mothers. For example, one adult female with a single yearling female spent all of the ice-free period of 1984 within 10 km of Cape Churchill. In 1985, the now independent two-year-old female returned to the same area and spent the summer and fall within the area used the previous year and was seen several times within 100 m of adult males.

Subadult females and subadult males occupy similar areas. Only during October, when subadult females were further inland, did they occupy different areas. The reasons for this separation may be caused by the distribution of pregnant four-year-old females that occupy areas further inland. Small differences between the regions used by subadult females and subadult males resulted in differences in their relationship with adult males. The relatively larger size of subadult males may make them less likely to be harassed by other bears and therefore they may tend to remain closer to the coast.

Subadult females were furthest inland during August and began moving back to coastal areas during September. The monthly pattern seen in the distance moved per day

was similar to that shown by family groups and adult males (lower during September). However, movement patterns differed in that subadult females did not show a tendency to remain in a single location over extended periods. This could be related to a general energy conservation strategy by reducing movements while still moving about to explore different areas. The exploring aspect of subadult females may be important later in life when locating appropriate areas for denning. Latour (1981a) noted that subadult females were more active than other groups in his study area at Cape Churchill because they were approached more by other subadults and this may account for their tendency not to remain in a single area. The density of bears at the Cape Churchill area late in the fall is much higher than that found during earlier periods, but the avoidance of conspecifics probably influences movement patterns throughout the year.

Subadult females as a group only showed significant orientation during October and November as they moved northward along the coast to the areas between Churchill and Cape Churchill. As the sea ice forms first in this area it allows the animals earlier access to their primary habitat. The high density of bears using this area in the fall makes it unlikely that a subadult female could retain the possession of a seal if they managed to kill one. As the area of the sea ice increased and the density of bears decreased, the likelihood that a subadult could retain a kill would rise. Some subadult females and males apparently use the newly formed sea ice that rims the coast as a travel corridor as several are taken by Inuit along the Keewatin coast early in the fall and often within 2 or 3 weeks of their last sighting in the study area. These bears are already hunting successfully, as some of the hunter-killed bears have stomachs full of seal (M. Cattet personal communication).

Some subadults show a high degree of fidelity to the study area while they are young and later as adults. The Churchill dump attracts some subadult females every year while they are young and a few subsequently return with their own offspring. It was apparent from the data that the dump at Churchill strongly influenced the

movements of some individuals as they travelled substantial distances to reach it. Lunn and Stirling (1985) concluded that the nutritional benefit obtained by the bears feeding in the dump was not critical and did not influence survival or reproductive rates.

The distribution of denning habitat may be locally abundant, but centred only in specific areas. If denning habitat is limited in its general distribution, then the fidelity of subadult females to their natal area may be highly adaptive. Repeat visits to the same area would increase an individual's familiarity with the distribution of potential denning habitat and other resources. Surveys of the region north of Churchill have not found evidence of denning. The features of the Churchill denning area that make it suitable for denning may be related to the distribution of peat formations used during the summer as dens. Earth dens are not used throughout the winter and females construct a snow den at the same site. Higher latitude polar bear populations do not use earth dens, but the earlier arrival of snow may preclude their necessity.

The energetic and nutritional importance of foraging by subadult females during the ice-free period is unclear. Subadults fed on berries, carrion, and refuse when available, but the influence of food on distribution patterns and movements is unknown. The movements of subadult females do not appear to be strongly influenced by weight or age, except during October and November when the older and possibly pregnant subadult females were found further inland.

2.4.4 Adult males

Adult males as a group occupied a very narrow band of habitat along the coastal regions and as a result were separated from females of all age classes for much of the ice-free season. There appear to be several factors associated with the segregation of adult males and adult females.

The dominance of adult males over subordinate conspecifics and the threat of cannibalism has been considered to be a primary factor influencing the distribution

patterns of polar bears while on the sea ice (Stirling *et al.* 1975; Taylor *et al.* 1985). The conditions found during the ice-free period are vastly different from those found on the sea ice. Despite the similarities in the spatial relationship between bears of different age and sex classes throughout the year, the causes behind the separation may differ with time. Eisenberg (1981) considered that spacing behaviour may be phasic. Use of the coastal areas by adult males may be considered to be an optimal strategy for energy conservation as it is the area closest to the sea ice. The large size of adult males would make extensive movements energetically expensive. Adult males reach 95 percent of their final weight at roughly 13 years and are still rapidly growing until 7 or 8 years of age (Kingsley 1979). However, as a group, their larger size and ability to defend kills on the sea ice probably make them more efficient hunters and may be less nutritionally stressed than other bears during the ice-free period. The low number of adult males using the dump attests to their ability to accumulate adequate fat stores (Lunn and Stirling 1985). If adult males have sufficient fat stores to carry them through the ice-free period then the coastal region may simply represent the first area that they enter as they arrive off the sea ice and subsequently there may be no energetic benefit in travel to inland areas or the dump to forage.

Factors other than the simple conservation of energy appear to be important as there is a significant trend for adult males to move southward along the coast during July through August and to subsequently retrace their path northward later in the fall. Some of these movements represent a return trip of more than 150 km. Travelling to specific sites appears to be an important factor influencing the movement patterns of adult males and aggregations of adult males are prevalent at specific locations along the coast. Aggregating behaviour of reproductively mature males outside of the breeding season is a common phenomena in several species of large mammals including: lions (*Panthera leo*) (Schaller 1972), walrus (*Odobenus rosmarus*) (Fay 1981), sea otter (*Enhydra lutris*) (Kenyon 1981; Garshelis *et al.* 1984), mountain sheep (*Ovis* spp.)

(Geist 1971), and red deer (Clutton-Brock *et al.* 1982). The reasons for aggregation range widely from prey acquisition to predator avoidance. The close association between individuals at aggregation sites indicate that social interaction may be important for polar bears. Latour (1981b) thought that social play between adult male polar bears during the ice-free period may function to expose individuals to several conspecifics and allow the development of the ability to assess the fighting capability of others through visual cues. Latour (1980) thought that the development of a stable dominance relationship between adult males was unlikely given the limited amount of time that bears could interact. Although observations are limited early in the ice-free period, play between adult males appears to be concentrated later in the fall, possibly influenced by the cooler temperatures. Results from this study indicate that long-term fidelity to the study area and specific sites is common and given that adult males can be concentrated for more than four months every year it is conceivable that a loose dominance hierarchy may exist. The larger size of adult males found in aggregations may be evidence of some level of organization based on size. The aggregating males were approximately 60 kg (18 percent) heavier than males only seen alone and it is possible that this is detectable by other bears. Stirling (1974) reported that the relative size of polar bears is probably sufficient to determine dominance. Christian (1970) noted that social organization based on hierarchical rank between individuals, families, or coherent groups is a common mammalian theme. Accurately assessing opponents for resources may be advantageous in avoiding serious injury during conflicts for resources (*eg.* Clutton-Brock *et al.* 1979). As adult male polar bears can suffer substantial injury during conflicts on the sea ice, familiarity with conspecifics may reduce the frequency and intensity of interactions. Two major selective pressures have been suggested to explain the existence of group living in Carnivora: the need for assistance in killing large prey and for defence against attacks (review by Macdonald 1983). Neither of these factors are adequate to explain the current social behaviour of polar bears, a normally solitary carnivore that needs no

help in killing nor is liable to attack from anything it would require assistance in repelling.

Low concentrations of circulating testosterone, such as those found during the ice-free period, are usually associated with low levels of aggression (review by Brain 1979). A positive correlation between plasma testosterone levels and dominance position in all male groups of rhesus monkeys has been reported by Rose *et al.* (1971, 1972). The number of blood samples from the study area are too small to determine possible influences that testosterone levels may have on the degree of association or social interactions between individuals. The low level of variation and the similarity between the testosterone titres of adult males in the inland areas and along the coast may indicate that it is not influencing distribution patterns. The non-competitive conditions under which adult males spend the summer and fall and their low levels of aggression are conducive to the aggregation of individuals. Macdonald (1983) noted that if the costs of group membership or being part of an aggregation are small, then the advantages need not be great in return and may be nothing more than the avoidance of dispersal. Macdonald also argued that members of spatial groups, individuals that are likely to meet more often than expected by chance, are available to receive benefits that derive from higher levels of sociality. Aggregations of adult males may form because the costs of associating are low and potential benefits may accrue in future meetings. Some individuals were found at the same aggregation areas with some of the same individuals in both 1984 and 1985. Recurrent associations of individuals may be passive and a function of affinity to specific sites although insufficient information was available to determine this.

Residency at the coast, on prominent points, and on islands may assist in the thermoregulatory balance of adult male polar bears. The coastal region tends to be cooler than inland areas. The larger adult males, particularly those with thick subcutaneous fat deposits, are subject to heat stress and hyperthermia due to the

functional consequences of scaling and the insulatory properties of blubber (Hurst *et al.* 1982a,b; Øritsland 1970; Schmidt-Nielsen 1984). Wind is an important factor influencing the thermal budget of polar bears by altering convective heat loss (Best 1982). Cool breezes blowing off the water may make islands and points preferred areas for summering. Adult males are often seen swimming in the Bay during the summer and it is possible that this may aid thermoregulation during warm periods. The number of biting insects are generally lower along the coastal area and this may influence habitat selection. Adult male aggregations may occur primarily as a function of habitat selection by dominant males and subsequent tolerance of co-dominant animals.

It is possible that these aggregations form due to other benefits derived from being on points or islands. Marine mammal carrion drifting ashore along the coast could make the coastal region preferred habitat for adult males that could retain possession of a carcass. Furnell and Oolooyuk (1980) reported a case of successful predation by an adult male polar bear on a ringed seal during the open water period, but serum urea and creatinine ratios reported by Lunn (1985) and Ramsay (1986) and the minor importance ringed seals had in scats collected by Russell (1975) indicate that hunting for seals is not important during the summer.

The segregation of adult males and family groups is a function of inland movements by families and a lack of inland movement by adult males. Adult males in the inland area appeared to be of similar age and weight to individuals along the coast. Some adult males have been seen in the same inland location over several years. Spending the ice-free period in the inland areas may be a function of individuals finding suitable habitat for summering when young and showing site tenacity over time. Most adult males in the inland area are associated with the edges and peninsulas of lakes. The frequent use of summering pits and dens in the inland area, dug down to the permafrost, could represent a viable thermoregulatory option to residency along the coast. The weak correlation between distance inland and weight found during August was

probably a function of younger bears moving inland sooner than older bears.

It is unlikely that adult males are moving inland in search of cubs to prey upon. Infanticide as an adaptive strategy for males may function in instances where a male can terminate a female's investment in offspring fathered by other males and stimulate a rapid resumption of receptivity and subsequent breeding opportunity (Hrdy 1974; Bertram 1975; Packer and Pusey 1984). Taylor *et al.* (1985) thought that infanticide may be a reproductive strategy of adult males during the breeding season, but the substantial temporal and spatial distance between the ice-free period and the breeding season make this a questionable reproductive strategy at this time of the year. Young Belding's ground squirrels (*Spermophilus beldingi*) appear to be infanticidal and cannibalistic for the nutritional benefit (Sherman 1981). Given, the high energetic costs of an adult male moving into the inland area, to actively pursue the more mobile family groups, the risk of severe injury, and the small size of cubs, it appears that the net benefit of infanticide for energetic reasons is limited.

Adult males as a group were least active during September and a large portion were inactive throughout the study period; indicative of an energy conservation strategy. The importance of food during the summer is unknown. Two adult males handled in September 1986 were found to be using *V. uliginosum* berries in the inland area, but moss was generally more prevalent in the few scats analyzed. Mosses are low in caloric content, but are important in mineral cycling (Forman 1968) and it is possible that intake of vitamins and mineral may be influencing forage species. Most adult males do not move into the inland area and appear to have sufficient fat stores to carry them through the ice-free period. The substantial energetic cost of moving to the inland area may outweigh the energetic intake. Residency along the coast and moving inland are apparently variations of the same strategy and given the non-competitive conditions during the ice-free period it is possible that neither strategy is strongly selected for or against. The exact conditions under which the social organization of polar bears evolved

are unknown and therefore the patterns displayed may be related to factors no longer present.

2.4.5 Subadult males

The distribution of subadult males within the study area was similar to that seen for subadult females. Differences were evident during October when subadult males were closer to the coast. Subadult males were separated from adult males only in August, but later in the ice-free period, after returning to the coast, they tended to occupy the same areas as adult males. This contrasts with the situation found in black and grizzly bears where subadult males avoid adult males and disperse when densities of adult males are high (Young and Ruff 1982; Glenn and Miller 1980; Jonkel and Cowan 1971; Pearson 1975). This may be due to changes in the levels of aggression of adult males or changes in perceived threat by subadult males. Concentrations of grizzly bears feeding on a salmon run show a change in the nature of aggressive interactions over time, using less intensive threats later in the season (Stonorov and Stokes 1972). Stonorov and Stokes (1972) also stated that behavioural changes by subordinates could inhibit attack. The conditions found in the study area are far less competitive than those found during active feeding periods, but it is probable that the nature of interactions change over the ice-free period. In October and early November 1984, at Cape Churchill, subadult males were often seen in close proximity to adult males, but generally rested in separate areas. Lunn and Stirling (1985) observed that independent yearling males did not rest along the coastal area.

Subadult males were found furthest inland during August, but moved back towards the coast sooner than other groups, with the exception of subadult females. During August, the negative correlation between age and distance from the coast and weight and distance from the coast indicated that it was the younger and subsequently lighter bears that were in the inland area. This may be related to younger bears showing

fidelity to areas that were used when with their mothers or a function of real or perceived danger resulting from the large number of adult males along the coast. The early return to the coast may be a function of two factors, not necessarily exclusive. Firstly, subadults may be displaced from the inland areas by an influx of dominant animals. Secondly, the Churchill dump influences the movements of many subadults that have used it in the past and the early return to the coast may be partially associated with movements towards the dump, although most bears do not arrive there until October. The timing of the return to the coast may vary annually for bears that use the dump as a supplemental food source. In 1983, polar bears arrived at the Churchill dump a month earlier than normal. Lunn and Stirling (1985) considered the poorer condition of individuals to be the cause. During 1984, all bears were in good condition again and very few used the dump.

Subadult males, unlike all other groups, did not show monthly variation in the distance moved per day. Given that the magnitude of movements were similar between all groups, with few exceptions, the reasons that subadult males moved constantly are unknown. Age and weight did not appear to influence movement patterns of subadult males. The constant moving by subadult males may be related to dispersal patterns at different times of the year. Dispersal in polar bear populations occurs predominantly on the sea ice. Most of the tag returns from bears killed in the Northwest Territories, Quebec, and the exchange between the study population and the Ontario population were subadult males when first handled in the study area. The typical mammalian pattern of dispersal by males (Eisenberg 1981) may also hold for polar bears to some degree. The high proportion of subadult males in the harvest along the Keewatin coast is a function of early and extensive movements along the young sea ice as it rims the coast. There are benefits and risks associated with dispersal (review by Horn 1983). The conditions during the ice-free period are such that the benefits of dispersal by subadult males may be limited and the mechanisms acting to induce dispersal may not function at this time.

There may be advantages in being philopatric if other areas do not offer the same benefits that known areas do. The manner in which polar bears navigate is unknown, but it is essential that they manage to return to land as the sea ice melts. Therefore, the high degree of fidelity that subadult males show to the study area probably relates to navigational patterns learned from their mothers.

Movement patterns of subadult males as a group demonstrated a lack of orientation over most months. Subadults do not appear to be as directed in their movements as older bears. It is probable that movement patterns during the ice-free period are learned over several years and the roaming of subadults exposes them to a wide variety of habitat, some of which is incorporated into their summer range as adults. Lunn and Stirling (1985) noted that subadult males stop using the dump at about 5 or 6 years of age due to decreased energetic demands. As this is also the age at which subadults begin to show up in adult male aggregations, it is probable that social and energetic factors are influencing their shift in habitat. The random and continuous movements of subadults may be due to active avoidance of conspecifics, but the high degree of association between adult males and subadult males makes this unlikely.

Subadult male movement patterns may be associated with searching for food. Evidence from this study indicates that subadults do make use of a wide range of food sources. Lunn and Stirling (1985) calculated that hunting geese was probably not efficient for polar bears, but their calculations were based on a 320 kg bear which is considerably higher than the 180 kg mean weight found for subadult males in 1985. Bears are opportunistic feeders, but the importance that feeding has on the movements of subadult males is unknown and requires further study.

2.4.6 Overview

Polar bears demonstrate a pattern of on-land distribution and movement over time that differs with the age, sex, and reproductive class. Despite the wide degree of

variation between the different groups and between individuals there are some common features. The distribution patterns of polar bears during the ice-free period is similar to that found on the sea ice. The factors influencing distribution patterns during the summer and fall are different than those acting on the sea ice, but not necessarily independent.

Historically, polar bears were thought to roam widely and lead a nomadic life. However, polar bears during the ice-free period show a high degree of fidelity to the study area, both in a single-season and over several years. The mechanisms by which polar bears navigate are unknown. It is clear that many bears, particularly adult males, are orientating themselves along the coast. However, other means of navigation must be used, both to return to the study area each summer and within the study area, given the observed patterns of fidelity. Rogers (1987) found that translocated black bears were able to home back to their original home range and did not use expanding search patterns or random movements. Translocated polar bears have travelled distances of over 400 km to return to Churchill (Stirling *et al.* 1977). Problem animals regularly travelled over 80 km after translocation during the course of this study.

Polar bears of all age and sex classes appear to demonstrate a degree of philopatry to the study area and dispersal does not appear to be common in any age or sex class. Immigration into the study area appears to be limited. The exchange between the Ontario and Manitoba sub-populations appears to be the result of some bears making periodic visits outside of their normal summering areas, possibly as a function of ice break-up patterns. Based on aerial survey information, Prevett and Kolenosky (1982) suggested that there was an annual exchange of bears between Manitoba and Ontario. However, the results of this study indicated that polar bears show a high degree of fidelity over many years and within a single year to the study area and that extensive movements between Manitoba and Ontario do not occur.

Several studies have demonstrated that polar bears show fidelity to feeding areas on the sea ice in the spring (Stirling *et al.* 1978, 1984; Lentfer 1983; Schweinsburg *et al.* 1982). Stirling *et al.* (1978) reported a mean relocation distance for bears captured or harvested one or more years later of 98 km and 137 km for males and females, respectively. The benefits of fidelity to the study area and site tenacity are probably similar to those derived by other animals from home ranges and territories. Polar bears are highly mobile, but there are advantages to gaining familiarity within a home range and learning the distribution of resources. Natal area fidelity does occur, although insufficient information is available to determine the extent. Adult females may den in the Churchill area, not because of any particular feature of the area, but due to its proximity to areas important for feeding and patterns of sea ice beak-up.

The effects of Inuit hunting on the distribution patterns of the bears in the Hudson Bay are unknown. Over 60 bears are harvested annually in the Keewatin area and it is possible that bears inhabiting the areas north of Churchill are more susceptible to hunting due to the presence of several Inuit communities. This may function to reduce the density of bears in localized areas, but it is unlikely to result in the current pattern of distribution seen during the ice-free period. There has been no hunting of polar bears in Manitoba in recent years.

It is probable that the sea ice near the study area is productive for hunting seals and the study area represents the energetically most efficient place to spend the ice-free period. The distribution of ringed seals and bearded seals is not continuous and areas of high and low densities do occur (Stirling *et al.* 1982; Kingsley *et al.* 1985). Information on the distribution of seals is limited in the Hudson Bay area, but the density of ringed seals is variable (Smith 1975) and probably exerts a strong influence on the distribution of polar bears. The separation of the Ontario and Manitoba sub-populations may be a function of different hunting areas in the winter and spring. Few bears from the study area appear to use the areas in eastern Hudson Bay. Less than 1 percent (1/270) of the

annual harvest of 25 bears in the Belcher Islands have been handled in the study area. However, of the 73 bears handled along the Ontario coast and James Bay between 1967 and 1975, 23 percent (17/73) were harvested in the Belcher Islands, Ontario, or along the Quebec coast.

The distribution of polar bears during the ice-free period indicates that the selection of specific habitats is important. There are large areas, that despite extensive surveying, are not used by the bears. In general, polar bears do not rest in wet areas. Bears in the inland areas utilize dry patches of lichen or habitat raised above the sodden tundra. Along the coast, the drier sandy or gravel beaches are used more frequently than the wetter areas. This may partially account for the higher density of bears along the north coast, as areas further south are much wetter. Socially dominant animals generally occupy the most desirable habitat available (Christian 1970), but the desirable features of an area are specific to the needs of the individual. Schweinsburg *et al.* (1982) noted that adult male polar bears were less likely to move onto land during the summer in the Lancaster Sound area and tended to spend the summer on ice floes as long as possible. They thought that summer retreats used by females and subadult males may be important to the survival of smaller or less experienced bears. It is possible that the floe ice provides benefits similar to the coastal areas used by adult males in western Hudson Bay.

The movement patterns of all groups of polar bears on land during the ice-free period demonstrated movements much below those recorded on the sea ice. Daily movements of 17 km (S.E.=2; n=70) were found for seven different adult females on the sea ice in the Beaufort Sea throughout the year (calculated from Amstrup 1986). Median daily movements during the ice-free period are predominantly less than 2 km per day and is probably reflective of a general energy conservation strategy.

Mechanisms that space carnivores over an area are often a function of social, environmental, and resource factors. Macdonald (1983) argued that resource dispersion

is fundamental to the spacing and structure of carnivore society. The conditions during the ice-free period are different from those found on the sea ice and yet there is similarity in the segregation patterns. Physiological constraints, imposed by a lack of sufficient food during the ice-free period and different energetic demands on different animals, may make energy conservation or body fat the resource that drives social organization. Nearly all bears lose weight while onshore (Lunn and Stirling 1985). The rate at which body reserves are used may influence the condition that a polar bear is in when it returns to the sea ice. The late fall condition of a bear may affect subsequent survival and reproductive success, as the early winter period is not believed to be a period of high food availability. The spatial and temporal segregation of polar bears during the ice-free period is a system that permits a normally solitary species to spend a non-competitive season, in relatively high concentrations, and conserve energy stores.

Additional factors, unique to different individuals and groups, influence movement patterns and distribution. The importance of learned behaviour in polar bears is unknown, but they are intelligent animals with a flexible social system that is typical of carnivores in general.

Table 2-1. Polar bears handled and number of locations obtained for bears of different age, sex, and reproductive classes for July-November, 1966-1985.

	Handlings		Relocations	
	n	%	*n*	%
Females with cubs-of-the-year	149	11	117	13
Females with yearlings	51	4	45	5
Lone adult females	87	7	135	15
Subadult females	314	23	52	6
Total females	601	45	349	39
Adult males	283	21	465	51
Subadult males	456	34	88	10
Total males	739	55	553	61
Overall total	1340	100	902	100

Table 2-2. Distance(km) from the coast for polar bears of different age, sex, and reproductive classes for July-November, 1966-1985.

Group	Month	*n*	Mean(S.E.)	Median	Range
Family groups	Jul.	7	3.1(1.3)	2.8	7.8
Lone adult females		5	7.7(6.1)	2.8	31.8
Subadult females		5	0.8(0.4)	0.9	2.0
Adult males		38	1.2(0.6)	0.0	18.6
Subadult males		4	0.7(0.4)	0.5	1.8
Family groups	Aug.	89	19.9(2.0)	18.1	57.2
Lone adult females		44	16.5(3.1)	2.2	63.0
Subadult females		40	15.2(3.4)	2.0	65.6
Adult males		201	2.4(0.4)	0.9	49.5
Subadult males		53	10.7(2.3)	1.8	62.0
Family groups	Sep.	45	17.3(2.3)	12.6	56.9
Lone adult females		31	27.9(3.9)	28.3	83.6
Subadult females		37	6.9(2.0)	1.8	51.0
Adult males		146	3.4(0.6)	1.0	52.3
Subadult males		46	5.2(1.8)	1.0	57.0
Family groups	Oct.	143	21.3(1.6)	17.5	58.0
Lone adult females		91	34.2(1.9)	36.2	65.1
Subadult females		183	5.8(0.9)	1.8	60.7
Adult males		234	4.9(0.8)	0.9	61.4
Subadult males		247	3.1(0.6)	0.9	81.4
Family groups	Nov.	78	6.4(1.4)	1.8	58.2
Lone adult females		51	18.9(3.0)	6.9	65.5
Subadult females		101	2.1(0.5)	0.9	30.1
Adult males		129	2.1(0.6)	0.0	56.1
Subadult males		194	1.2(0.1)	1.8	15.7

Table 2-3. Mann-Whitney *U*-test results for differences in the distance(km) from the coast between 1984 and 1985 for polar bears of different age, sex, and reproductive classes for July-November.

		1984		1985			
Group	Month	*n*	Mean(S.E.)	*n*	Mean(S.E.)	*U*-Stat	*P*
Family groups	Jul.	5	2.2(1.5)	2	5.2(2.4)	7.0	0.422
	Aug.	30	15.6(2.8)	15	17.6(4.7)	244.0	0.647
	Sep.	31	18.4(2.8)	8	24.4(5.6)	162.0	0.186
	Oct.	19	14.5(3.6)	20	21.2(4.0)	243.0	0.136
	Nov.	9	4.1(1.5)	7	1.4(0.3)	10.5	0.026
Lone adult females	Jul.	3	1.9(0.9)	1	0.9(0.0)	-	-
	Aug.	19	10.7(3.9)	13	19.5(6.9)	155.0	0.211
	Sep.	14	22.7(5.0)	4	44.0(5.1)	48.0	0.034
	Oct.	14	20.6(4.3)	21	27.6(4.2)	117.5	0.320
	Nov.	4	23.1(9.3)	9	24.2(7.1)	18.0	1.000
Subadult females	Jul.	2	0.0(0.0)	2	1.5(0.6)	4.0	0.102
	Aug.	15	7.6(3.6)	17	15.6(5.4)	147.0	0.459
	Sep.	9	9.6(3.5)	8	10.5(6.3)	33.0	0.772
	Oct.	10	5.2(3.1)	29	9.2(2.9)	127.0	0.556
	Nov.	2	15.9(14.1)	16	2.6(1.0)	7.0	0.150
Adult males	Jul.	30	1.5(0.7)	6	0.5(0.2)	85.5	0.828
	Aug.	120	2.7(0.6)	68	1.3(0.4)	4022.0	0.864
	Sep.	77	3.4(0.9)	51	3.3(0.9)	1646.5	0.113
	Oct.	45	1.0(0.3)	56	3.6(1.2)	1556.0	0.037
	Nov.	22	1.7(0.8)	22	3.6(2.5)	249.0	0.864
Subadult males	Jul.	2	0.5(0.5)	2	0.9(0.9)	2.5	0.683
	Aug.	23	8.8(3.1)	9	10.9(5.8)	99.5	0.866
	Sep.	9	6.7(6.3)	11	12.3(5.1)	80.5	0.017
	Oct.	14	4.9(4.0)	30	8.6(3.4)	248.5	0.314
	Nov.	3	1.5(0.3)	24	1.8(0.6)	32.0	0.737

Table 2-4. Comparison of age(years) and weights(kg) of polar bears of different age and sex classes captured during July through September, 1984 and 1985.

		1984		1985			
Group		*n*	Mean(S.E.)	*n*	Mean(S.E.)	*t*	*P*
Family groups	Age	21	10.4(0.9)	13	12.1(0.9)	-1.24	0.226
	Weight	21	180(6)	13	178(10)	0.15	0.885
Lone adult females	Age	12	11.5(1.6)	8	13.8(2.7)	-0.76	0.454
	Weight	12	270(27)	8	218(14)	1.47	0.160
Subadult females	Age	15	2.4(0.3)	13	2.5(0.2)	-0.41	0.686
	Weight	15	144(10)	13	133(5)	0.92	0.366
Adult males	Age	62	12.1(0.6)	36	13.6(0.8)	-1.38	0.172
	Weight	62	372(12)	36	359(13)	0.70	0.486
Subadult males	Age	15	2.9(0.2)	13	2.7(0.2)	0.55	0.590
	Weight	15	212(14)	13	180(16)	1.52	0.141

Table 2-5. Multiple comparison test results for differences in the distance from the coast between polar bears of different age, sex, and reproductive status for August-November, 1966-1985.

Group		Family groups		Lone adult females		Subadult females		Adult males	
	Month	Z-Stat	d.f.	Z-Stat	d.f.	Z-Stat	d.f.	Z-Stat	d.f.
Lone adult females	Aug.	2.11	44,89						
	Sep.	1.58	31,45						
	Oct.	3.42*	91,143						
	Nov.	0.85	51,78						
Subadult females	Aug.	1.07	40,89	0.85	40,44				
	Sep.	3.31*	37,45	4.53*	37,31				
	Oct.	7.22*	183,143	9.86*	183,91				
	Nov.	3.50*	101,78	3.96*	101,51				
Adult males	Aug.	8.48*	201,89	4.15*	201,44	5.06*	201,40		
	Sep.	6.35*	146,45	7.34*	146,31	1.90	146,37		
	Oct.	10.13*	234,143	12.42*	234,91	2.73	234,183		
	Nov.	5.37*	129,78	5.58*	129,51	1.82	129,101		
Subadult males	Aug.	2.45	53,89	0.18	53,44	1.06	53,40	4.24*	53,201
	Sep.	4.62*	46,45	5.75*	46,31	1.06	46,37	0.68	46,146
	Oct.	10.51*	247,143	12.75*	247,91	3.07*	247,183	0.32	247,243
	Nov.	4.04*	194,78	4.42*	194,51	0.11	194,101	2.00	194,129

* significant at $P \leq 0.05$.

Table 2-6. Distance(km) from the coast for polar bears of different age, sex, and reproductive classes for July-November, 1984 and 1985, as determined by radio tracking.

Group	Month	*n*	Mean(S.E.)	Median	Range
Family groups	Jul.	5	1.9(1.3)	0.5	7.6
Lone adult females		3	1.9(0.9)	2.8	2.8
Subadult females		2	1.5(0.6)	1.5	1.1
Adult males		3	0.3(0.3)	0.0	0.9
Subadult males		2	0.9(0.9)	0.9	1.8
Family groups	Aug.	36	17.9(2.8)	13.9	49.3
Lone adult females		27	15.8(4.3)	1.0	63.0
Subadult females		20	9.1(3.9)	1.4	62.9
Adult males		35	5.4(1.4)	0.9	21.1
Subadult males		8	20.3(5.6)	22.0	51.1
Family groups	Sep.	33	20.6(2.7)	16.9	56.9
Lone adult females		16	25.7(5.0)	26.1	65.1
Subadult females		15	9.8(3.7)	3.4	51.0
Adult males		34	7.8(2.0)	1.8	52.3
Subadult males		12	17.7(5.8)	10.2	57.0
Family groups	Oct.	35	18.7(2.8)	15.3	53.5
Lone adult females		21	27.3(4.0)	25.9	63.4
Subadult females		27	10.9(3.2)	1.8	51.2
Adult males		37	4.9(1.8)	1.0	61.4
Subadult males		15	16.0(6.7)	0.0	81.4
Family groups	Nov.	14	5.4(2.5)	2.0	32.3
Lone adult females		11	27.9(5.7)	25.9	60.4
Subadult females		9	6.3(3.5)	1.8	30.1
Adult males		17	2.3(1.0)	1.0	17.5
Subadult males		11	2.1(1.4)	0.9	15.7

Table 2-7. Comparison of distance from the coast(km) for radio tagged polar bears in 1984 and 1985 to all other sightings and locations from 1966 to 1985.

		1966-1985		Radio			
Group	Month	*n*	Mean(S.E.)	*n*	Mean(S.E.)	*U*-Stat	*P*
Family groups	Aug.	53	21.2(2.8)	36	17.9(2.8)	928.5	0.831
	Sep.	12	8.3(3.8)	33	20.6(2.7)	286.0	0.024
	Oct.	108	22.3(2.0)	35	18.7(2.8)	1843.5	0.826
	Nov.	64	7.1(1.7)	14	5.4(2.5)	574.5	0.090
Lone adult females	Aug.	17	20.7(4.7)	27	15.8(4.3)	166.5	0.123
	Sep.	15	30.2(6.1)	16	25.7(5.0)	113.0	0.782
	Oct.	70	35.2(2.2)	21	27.3(4.0)	544.5	0.073
	Nov.	40	16.5(3.4)	11	27.9(5.7)	313.0	0.029
Subadult females	Aug.	20	21.3(5.3)	20	9.1(3.9)	123.5	0.038
	Sep.	22	3.9(1.9)	15	9.8(3.7)	222.5	0.066
	Oct.	156	4.9(0.9)	27	10.9(3.2)	2387.0	0.268
	Nov.	92	1.7(0.4)	9	6.3(3.5)	527.5	0.147
Adult males	Aug.	166	1.8(0.5)	35	5.4(1.4)	3430.5	0.075
	Sep.	112	2.0(0.5)	34	7.8(2.0)	2564.0	0.002
	Oct.	197	4.9(0.9)	37	4.9(1.8)	4376.5	0.045
	Nov.	112	1.6(0.5)	17	2.3(1.0)	1231.0	0.034
Subadult males	Aug.	45	9.0(2.5)	8	20.3(5.6)	242.0	0.120
	Sep.	34	1.4(0.4)	12	17.7(5.8)	316.5	0.004
	Oct.	232	2.3(0.5)	15	16.0(6.7)	1799.5	0.812
	Nov.	183	1.1(0.1)	11	2.1(1.4)	919.0	0.596

Table 2-8. Multiple comparison test results for differences in the distance from the coast between radio tagged polar bears of different age, sex, and reproductive status for August-November, 1984 and 1985.

Group		Family groups		Lone adult females		Subadult females		Adult males	
	Month	Z-Stat	d.f.	Z-Stat	d.f.	Z-Stat	d.f.	Z-Stat	d.f.
Lone adult females	Aug.	1.91	27,36						
	Sep.	0.86	16,33						
	Oct.	1.22	21,35						
	Nov.	2.72	11,14						
Subadult females	Aug.	2.21	20,36	0.44	20,27				
	Sep.	2.22	15,33	2.65	15,16				
	Oct.	2.83*	27,35	3.65*	27,21				
	Nov.	0.78	9,14	3.18*	9,11				
Adult males	Aug.	3.43*	35,36	1.28	35,27	0.71	35,20		
	Sep.	3.52*	34,33	3.70*	34,16	0.55	34,15		
	Oct.	4.06*	37,35	4.74*	37,21	0.92	37,27		
	Nov.	1.66	17,14	4.38*	17,11	0.65	17,9		
Subadult males	Aug.	0.17	8,36	1.37	8,27	1.63	8,20	2.25	8,35
	Sep.	0.90	12,33	1.48	12,16	1.00	12,15	1.66	12,34
	Oct.	2.62	15,35	3.39*	15,21	0.26	15,27	0.49	15,37
	Nov.	2.19	11,14	4.64*	11,11	1.22	11,9	0.73	11,17

* significant at $P \leq 0.05$.

Table 2-9. Mann-Whitney *U*-test results for differences in the distance(km) from the coast between adult females with cubs-of-the-year and adult females with yearlings for July-November, 1966-1985.

	Jul.	Aug.	Sep.	Oct.	Nov.
Females with cubs-of-the-year					
n	6	61	35	98	66
Mean(S.E.)	3.6(1.4)	20.2(2.4)	17.0(2.5)	21.3(1.9)	6.7(1.7)
Median	3.1	18.4	12.6	18.7	1.8
Range	7.8	57.2	56.9	58.0	58.2
Females with yearlings					
n	1	28	10	45	12
Mean(S.E.)	0.0(0.0)	19.1(3.7)	18.3(6.0)	21.5(3.1)	4.5(2.0)
Median	-	13.0	12.7	15.3	1.9
Range	-	53.0	43.3	57.7	21.3
U-Stat	-	902.5	188.0	2263.0	346.5
P	-	0.667	0.722	0.800	0.480

Table 2-10. Kruskal-Wallis test results for month-to-month differences in distance from the coast, July-November, 1966-1985.

Group	*H*-stat.	*P*	d.f.
Family groups	38.0	<0.001	4
Lone adult females	36.3	<0.001	4
Subadult females	20.8	<0.001	4
Adult males	18.9	0.001	4
Subadult males	18.6	0.001	4

Table 2-11. Kendall's coefficient of correlation(r) for age and weight with distance from the coast for July-November, 1966-1985.

Group	Month	*n*	Age r	Weight r
Family groups	Jul.	7	0.327	0.567
	Aug.	73	0.052	-0.159*
	Sep.	31	0.144	-0.379**
	Oct.	115	0.171**	-0.182**
	Nov.	61	0.179*	-0.033
Lone adult females	Jul.	3	0.500	0.000
	Aug.	32	0.250*	0.002
	Sep.	22	0.088	-0.143
	Oct.	64	0.098	0.174*
	Nov.	35	0.028	0.385**
Subadult females	Jul.	5	-0.386	0.000
	Aug.	40	0.026	-0.068
	Sep.	30	0.087	-0.134
	Oct.	147	0.193***	0.088
	Nov.	88	0.184*	0.135
Adult males	Jul.	38	-0.010	0.055
	Aug.	199	-0.214***	-0.118*
	Sep.	138	0.035	-0.035
	Oct.	224	0.024	0.084
	Nov.	128	0.090	-0.009
Subadult males	Jul.	4	1.000	0.548
	Aug.	52	-0.305**	-0.203*
	Sep.	42	-0.176	-0.042
	Oct.	210	0.022	-0.004
	Nov.	160	-0.084	-0.011

* $P \leq 0.05$ ** $P \leq 0.01$ *** $P \leq 0.001$

Table 2-12. Mann-Whitney *U*-test results for differences between 1984 and 1985 in the distance moved per day(km/day) for polar bears of different age, sex, and reproductive classes for July-November.

		1984		1985			
Group	Month	*n*	Mean(S.E.)	*n*	Mean(S.E.)	*U*-Stat	*P*
Family groups	Jul.	1	10.7(0.0)	0	-	-	-
	Aug.	14	2.9(1.4)	4	0.8(0.4)	40.0	0.202
	Sep.	17	0.9(0.4)	6	0.6(0.1)	36.0	0.293
	Oct.	10	1.1(0.3)	13	2.6(0.7)	34.0	0.054
	Nov.	0	-	0	-	-	-
Lone adult females	Jul.	1	0.3(0.0)	0	-	-	-
	Aug.	8	6.3(2.9)	5	2.3(0.7)	24.0	0.558
	Sep.	9	1.3(0.6)	4	0.6(0.3)	19.0	0.877
	Oct.	11	1.0(0.5)	19	3.0(1.0)	72.5	0.168
	Nov.	0	-	0	-	-	-
Subadult females	Jul.	0	-	1	1.4(0.0)	-	-
	Aug.	7	2.5(0.9)	7	3.2(0.6)	19.0	0.482
	Sep.	4	1.4(0.8)	7	1.8(1.3)	12.5	0.776
	Oct.	8	3.2(1.6)	12	2.9(0.7)	44.0	0.412
	Nov.	0	-	4	7.4(5.6)	-	-
Adult males	Jul.	10	2.4(0.9)	2	1.7(1.0)	8.0	0.667
	Aug.	102	1.5(0.2)	51	3.1(0.6)	2079.0	0.043
	Sep.	47	0.8(0.2)	42	1.0(0.3)	1037.0	0.680
	Oct.	36	1.3(0.2)	36	3.3(1.2)	526.0	0.167
	Nov.	4	3.6(0.8)	3	2.7(0.9)	7.0	0.724
Subadult males	Jul.	1	3.8(0.0)	0	-	-	-
	Aug.	15	1.4(0.4)	1	1.8(0.0)	4.0	0.447
	Sep.	5	1.2(0.6)	7	1.2(0.3)	17.0	0.935
	Oct.	8	1.9(0.7)	16	4.9(3.0)	55.0	0.581
	Nov.	0	-	4	16.0(12.3)	-	-

Table 2-13. Distance moved per day(km/day) for polar bears of different age, sex, and reproductive classes for July-November, 1966-1985.

Group	Month	*n*	Mean(S.E.)	Median	Range
Family groups	Jul.	1	10.7(0.0)	-	-
Lone adult females		1	0.3(0.0)	-	-
Subadult females		1	1.4(0.0)	-	-
Adult males		12	2.3(0.8)	1.4	9.6
Subadult males		1	3.8(0.0)	-	-
Family groups	Aug.	26	3.2(1.0)	1.6	21.1
Lone adult females		18	3.5(0.9)	2.3	12.4
Subadult females		14	2.9(0.5)	2.1	6.6
Adult males		158	2.1(0.3)	0.6	18.9
Subadult males		18	1.8(0.4)	1.4	7.2
Family groups	Sep.	29	0.9(0.3)	0.4	7.5
Lone adult females		15	1.2(0.4)	0.9	5.8
Subadult females		14	0.7(0.3)	0.3	3.6
Adult males		96	1.4(0.6)	0.3	52.4
Subadult males		13	2.0(0.6)	1.5	7.5
Family groups	Oct.	56	1.8(0.3)	1.1	14.8
Lone adult females		47	1.5(0.4)	0.5	15.8
Subadult females		80	2.6(0.8)	0.5	52.8
Adult males		132	2.1(0.4)	0.9	50.0
Subadult males		70	2.3(0.7)	0.8	49.1
Family groups	Nov.	13	2.0(1.1)	0.7	14.4
Lone adult females		14	2.0(0.8)	0.2	9.2
Subadult females		35	7.3(1.6)	3.5	43.2
Adult males		27	3.3(0.9)	2.0	22.3
Subadult males		57	4.6(1.4)	1.4	52.7

Table 2-14. Multiple comparison test results for differences in the distance moved per day between polar bears of different age, sex, and reproductive status for August and November, 1966-1985.

Group		Family groups		Lone adult females		Subadult females		Adult males	
	Month	Z-Stat	d.f.	Z-Stat	d.f.	Z-Stat	d.f.	Z-Stat	d.f.
Lone adult females	Aug.	0.88	18,26						
	Nov.	0.18	14,13						
Subadult females	Aug.	1.36	14,26	0.51	14,18				
	Nov.	2.00	35,13	2.27	35,14				
Adult males	Aug.	1.31	158,26	2.20	158,18	2.61	158,14		
	Nov.	1.03	27,13	1.26	27,14	1.18	27,35		
Subadult males	Aug.	0.36	18,26	1.14	18,18	1.57	18,14	0.67	18,158
	Nov.	0.23	57,13	0.01	57,14	3.29*	57,35	1.76	57,27

* significant at $P \leq 0.05$.

Table 2-15. Multiple comparison test results for differences in the distances moved per day between suspected pregnant females and other groups of polar bears August, October, and November, 1965-1985.

Group	Month	Z-Stat	d.f.
Family groups	Aug.	1.04	10,26
	Oct.	2.76	29,56
	Nov.	1.47	8,13
Subadult females	Aug.	0.15	10,14
	Oct.	1.40	29,80
	Nov.	3.43*	8,35
Adult males	Aug.	2.03	10,158
	Oct.	2.50	29,132
	Nov.	2.57	8,27
Subadult males	Aug.	1.26	10,18
	Oct.	1.10	29,70
	Nov.	1.57	8,57

* significant at $P \leq 0.05$.

Table 2-16. Mann-Whitney *U*-test results for differences between the distance moved per day by females with cubs-of-the-year and females with yearlings for July-November, 1966-1985.

	Jul.	Aug.	Sep.	Oct.	Nov.
Females with cubs-of-the-year					
n	1	17	19	40	11
Mean(S.E.)	10.7(-)	2.8(1.2)	1.2(0.4)	1.6(0.3)	2.1(1.3)
Range	0.0	21.1	7.5	2.0	14.4
Females with yearlings					
n	0	9	10	16	2
Mean(S.E.)	-	3.9(1.9)	0.4(0.1)	2.5(0.9)	1.9(1.9)
Range	-	18.2	0.9	3.6	3.8
U-stat.	-	63.0	110.5	270.5	11.5
P	-	0.467	0.477	0.369	0.921

Table 2-17. Kruskal-Wallis test results for variation between months in distance moved per day, August-November, 1966-1985.

Group	*H*-stat.	*P*	d.f.
Family groups	8.2	0.043	3
Lone adult females	6.6	0.085	3
Subadult females	20.2	<0.001	3
Adult males	22.9	<0.001	4
Subadult males	3.4	0.332	3

Table 2-18. Kendall's coefficient of correlation(r) for weight and age with distance moved per day for July-November, 1966-1985.

Group	Month	*n*	Age r	Weight r
Family groups	Jul.	1	-	-
	Aug.	23	0.054	0.235
	Sep.	23	0.154	0.112
	Oct.	42	0.017	-0.210*
	Nov.	11	0.255	0.257
Lone adult females	Jul.	1	-	-
	Aug.	14	0.012	0.011
	Sep.	12	-0.646**	-0.076
	Oct.	37	-0.112	-0.191
	Nov.	9	0.032	0.029
Subadult females	Jul.	1	-	-
	Aug.	14	-0.041	0.221
	Sep.	11	-0.609**	-0.404
	Oct.	76	0.058	-0.195*
	Nov.	35	0.058	-0.039
Adult males	Jul.	12	0.170	0.170
	Aug.	152	-0.036	-0.040
	Sep.	93	-0.124	-0.021
	Oct.	134	0.005	0.118*
	Nov.	31	0.135	-0.015
Subadult males	Jul.	1	-	-
	Aug.	18	-0.267	-0.099
	Sep.	15	-0.218	-0.168
	Oct.	70	0.113	0.074
	Nov.	57	0.137	0.022

* $P \leq 0.05$ ** $P \leq 0.01$

Table 2-19. The weighted mean distance moved per day(km/day) for individual bears in successive years.

Sex	Age*	Year	*n*	Mean(S.E.)	Year	*n*	Mean(S.E.)
M	6	1983	6	1.1(0.4)	1984	7	1.2(0.3)
M	13	1983	5	1.3(1.1)	1984	5	0.5(0.2)
M	5	1984	5	0.4(0.3)	1985	5	0.9(0.8)
M	7	1984	6	0.3(0.2)	1985	7	2.6(1.2)
M	8	1984	6	1.0(0.3)	1985	5	1.2(0.6)
M	8	1984	8	0.6(0.1)	1985	7	0.6(0.4)
M	9	1984	8	0.9(0.5)	1985	5	2.5(1.8)
M	11	1984	5	1.0(0.2)	1985	7	1.6(0.7)
M	12	1984	5	1.1(1.0)	1985	6	1.1(0.6)
M	12	1984	6	0.4(0.4)	1985	6	0.4(0.3)
M	16	1984	7	0.7(0.4)	1985	7	0.7(0.2)
M	18	1984	5	0.9(0.5)	1985	5	1.0(1.1)
F[1]	1	1984	5	0.2(0.1)	1985	6	1.3(0.4)
F[2]	8	1984	3	0.7(0.4)	1985	3	0.5(0.3)

* Age is given for the first of the two years.
[1] Yearling female with mother in 1984; lone 2 year old in 1985.
[2] Adult female with cubs-of-the-year in 1984; lone adult female in 1985.

Table 2-20. Proportion of tagged polar bears in capture and harvest samples from locations about Hudson Bay. Locations are listed clockwise starting at the study area.

Location	Capture sample and/or reported kill	Bears tagged in study area in sample	Proportion tagged
Study area	2047	831	0.406
Eskimo Point	271	57	0.210
Whale Cove	152	27	0.178
Rankin Inlet	144	18	0.125
Chesterfield Inlet	112	4	0.036
Coral Harbour	931	1	0.001
Southampton Island[1]	119	0	0.000
Quebec coast[2]	Unknown	7	-
Belcher Islands	270	1	0.004
Ontario	450	28	0.062
Southeast Manitoba[3]	39	8	0.205

[1]Government of N.W.T. study.
[2]Harvest was not recorded in Quebec.
[3]Area from the mouth of the Nelson River east to the Manitoba-Ontario border.

Table 2-21. Composition of 15 polar bear scats collected throughout the study area during September, 1986.

Group	Distance from coast(km)	Composition by Volumetric Category					
		Vaccinium uliginosum	moss	graminoids-cyperaceae	*Empetrum nigrum*	Aves	misc.
Adult female	48	95-100	tr-5	tr-5	-	-	tr-5
"	48	5-25	25-50	50-75	tr-5	-	tr-5
" [1]	54	tr-5	75-95	tr-5	5-25	-	tr-5
"	64	75-95	tr-5	-	-	tr-5	tr-5
"	68	95-100	-	-	-	-	-
" [1]	76	95-100	-	-	-	-	-
Subadult female	60	95-100	-	-	-	-	-
Adult male	0	-	-	95-100	-	-	-
"	20	75-95	-	-	tr-5	-	-
"	27	-	95-100	-	-	-	tr-5
"	28	-	95-100	tr-5	-	-	tr-5
"	38	25-50	50-75	tr-5	-	-	tr-5
Subadult male	0	-	-	-	-	95-100	-
"	0	tr-5	-	tr-5	-	95-100	-
"	42	95-100	-	-	-	-	-

[1]suspected to be pregnant; all other adult females were accompanied by cubs.

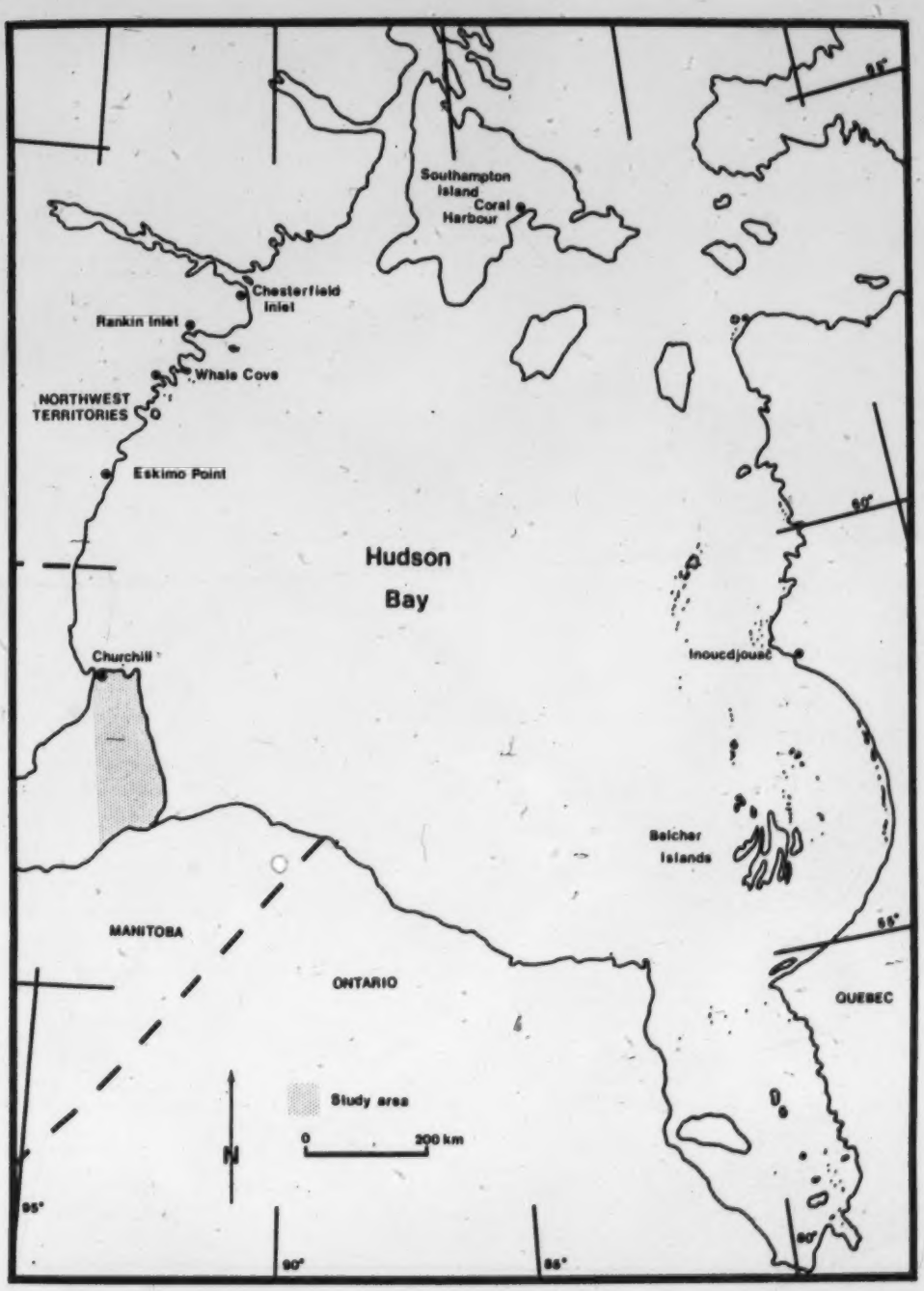

Figure 2-1. Map of Hudson Bay including the study area and locations mentioned in the text.

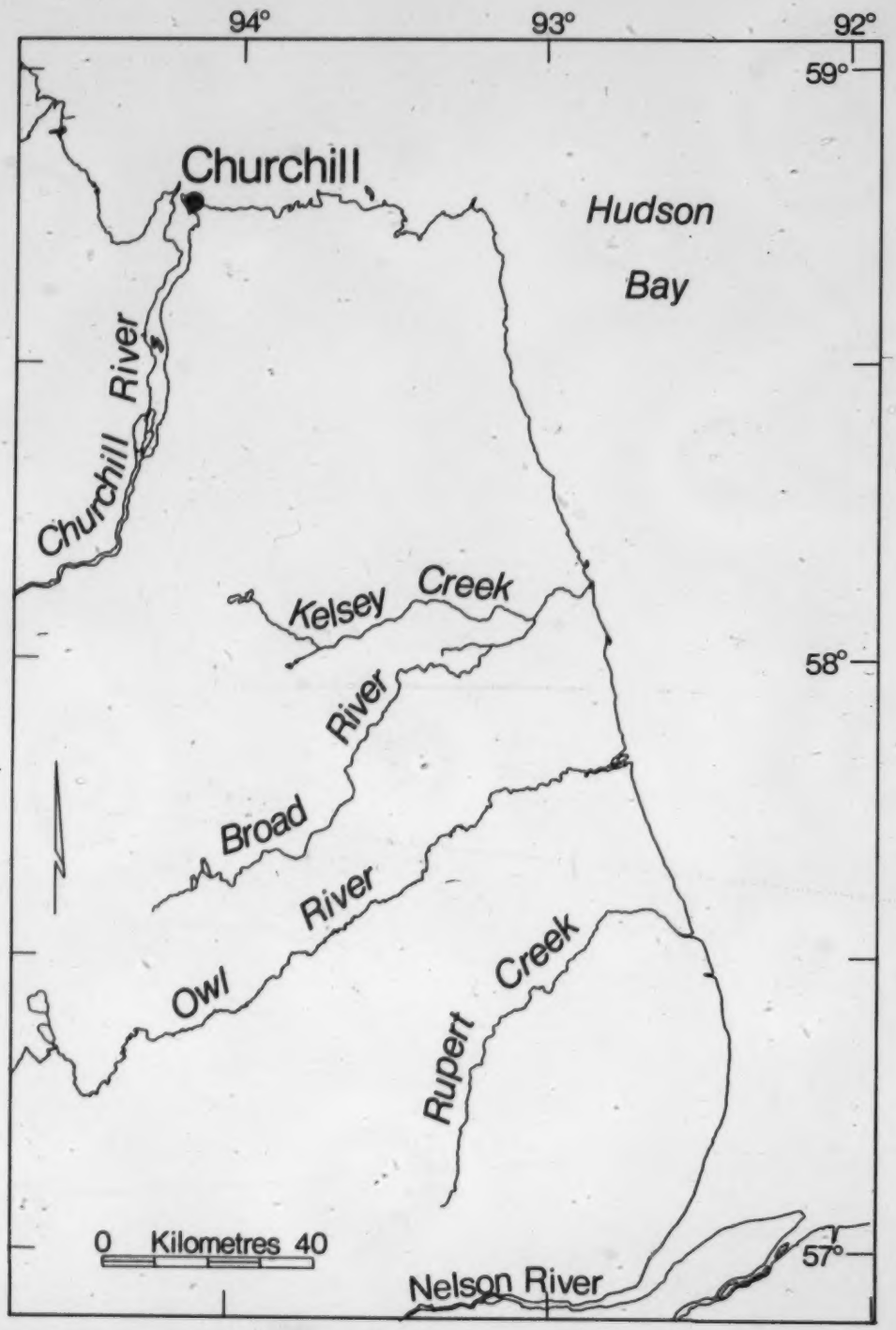

Figure 2-2. Details of the study area.

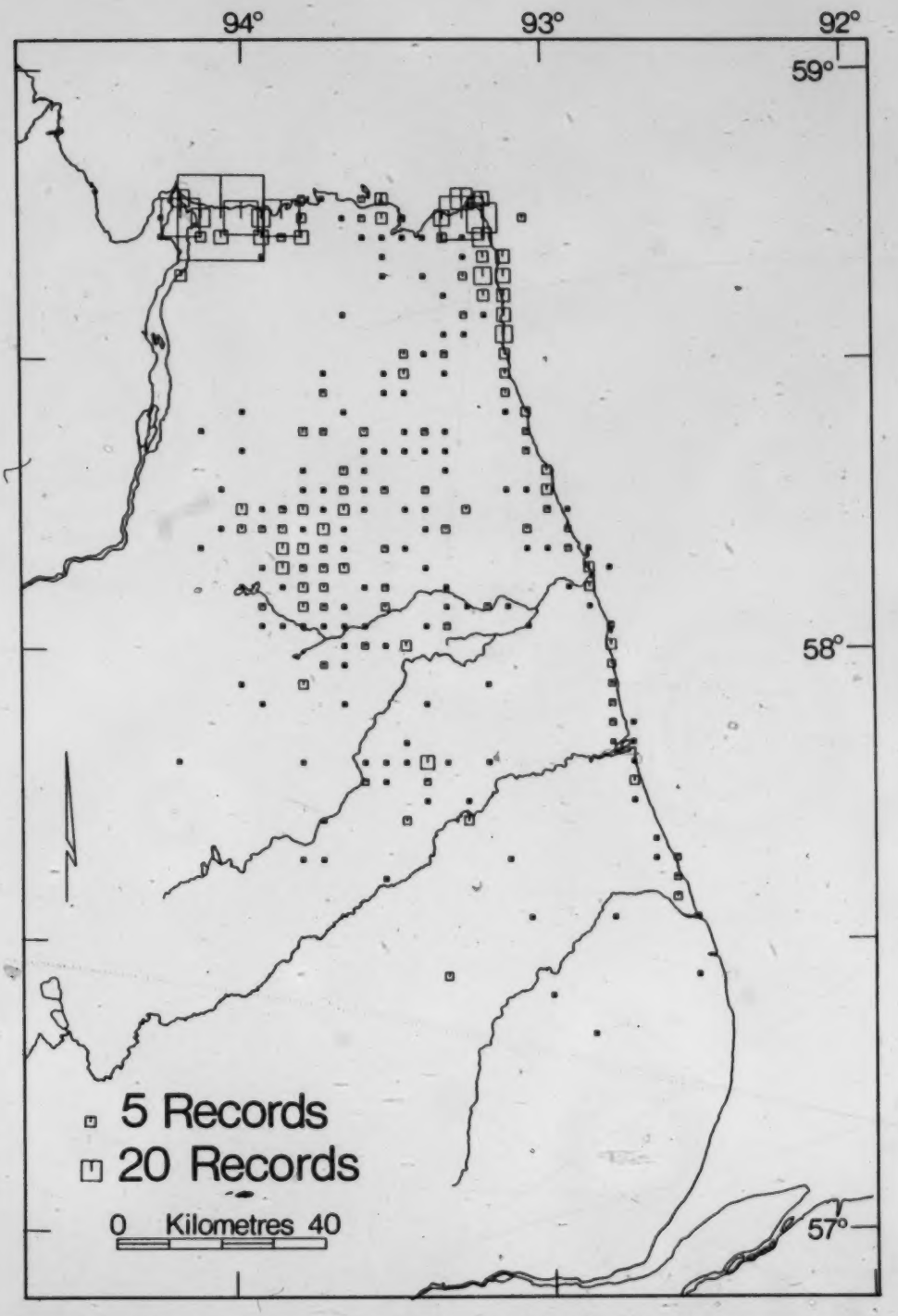

Figure 2-3. Map of capture capture locations of bears handled July through November, 1966-1985.

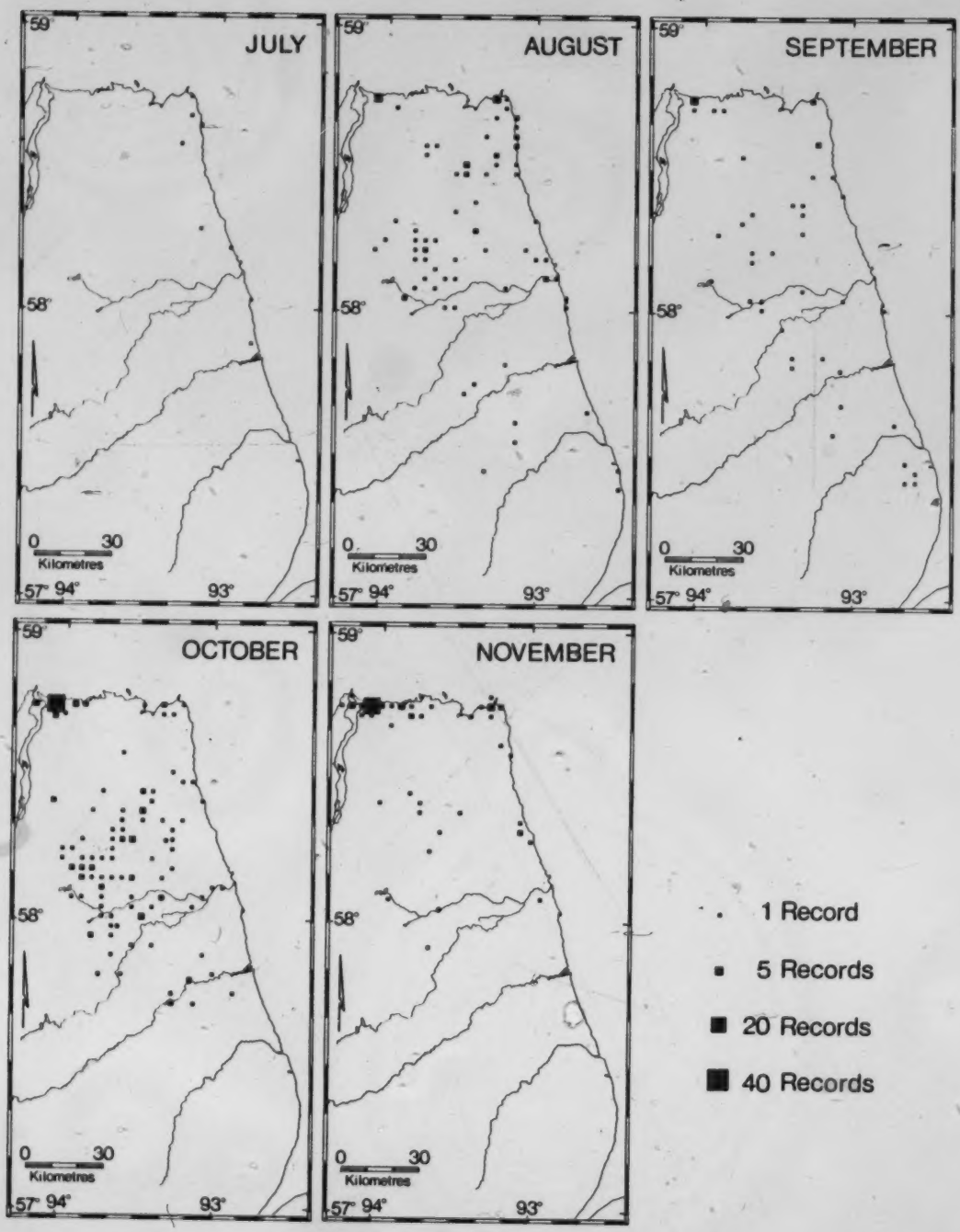

Figure 2-4. Map of monthly distribution patterns of family groups, July through November, 1966-1985.

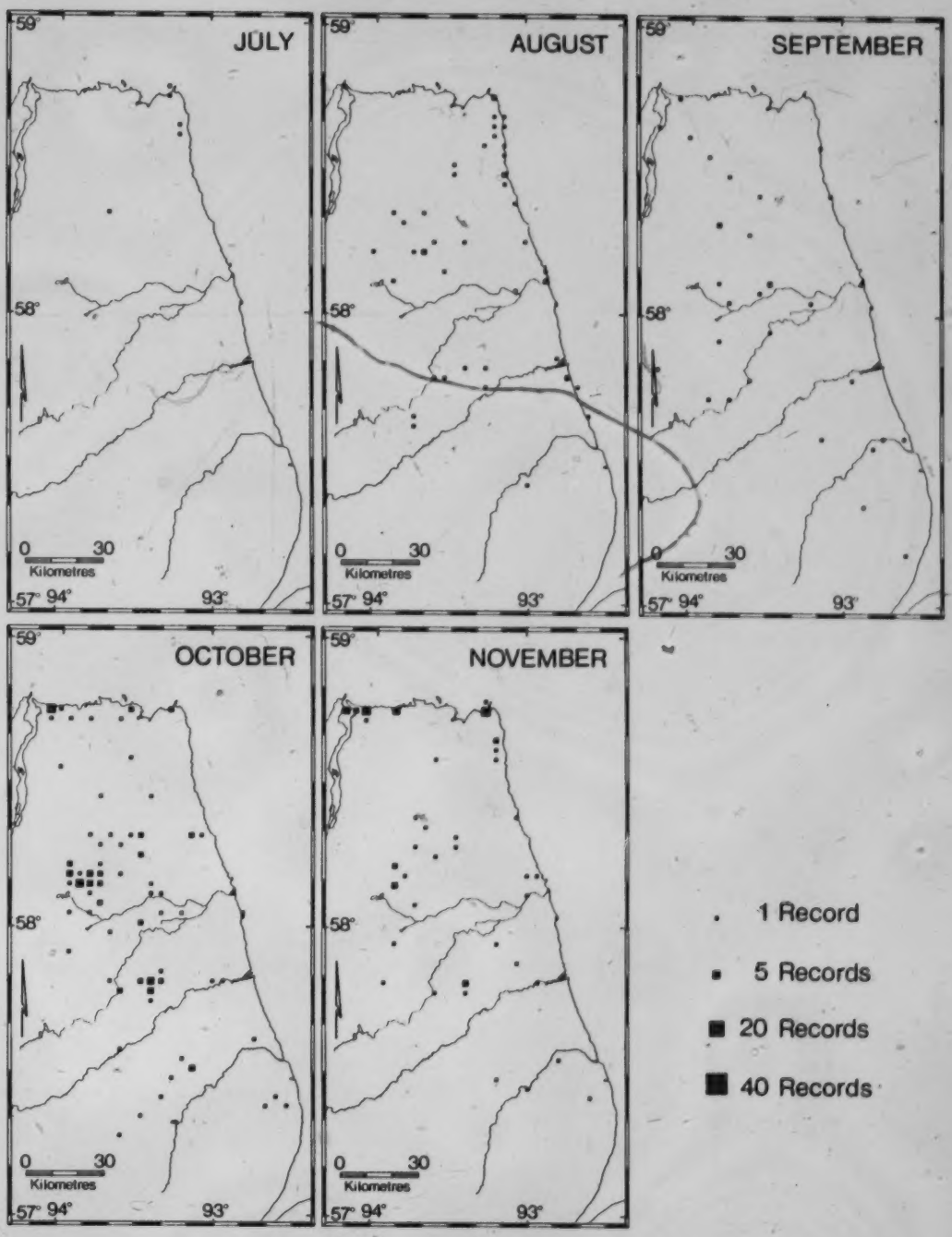

Figure 2-5. Map of monthly distribution patterns of lone adult females, July through November, 1966-1985.

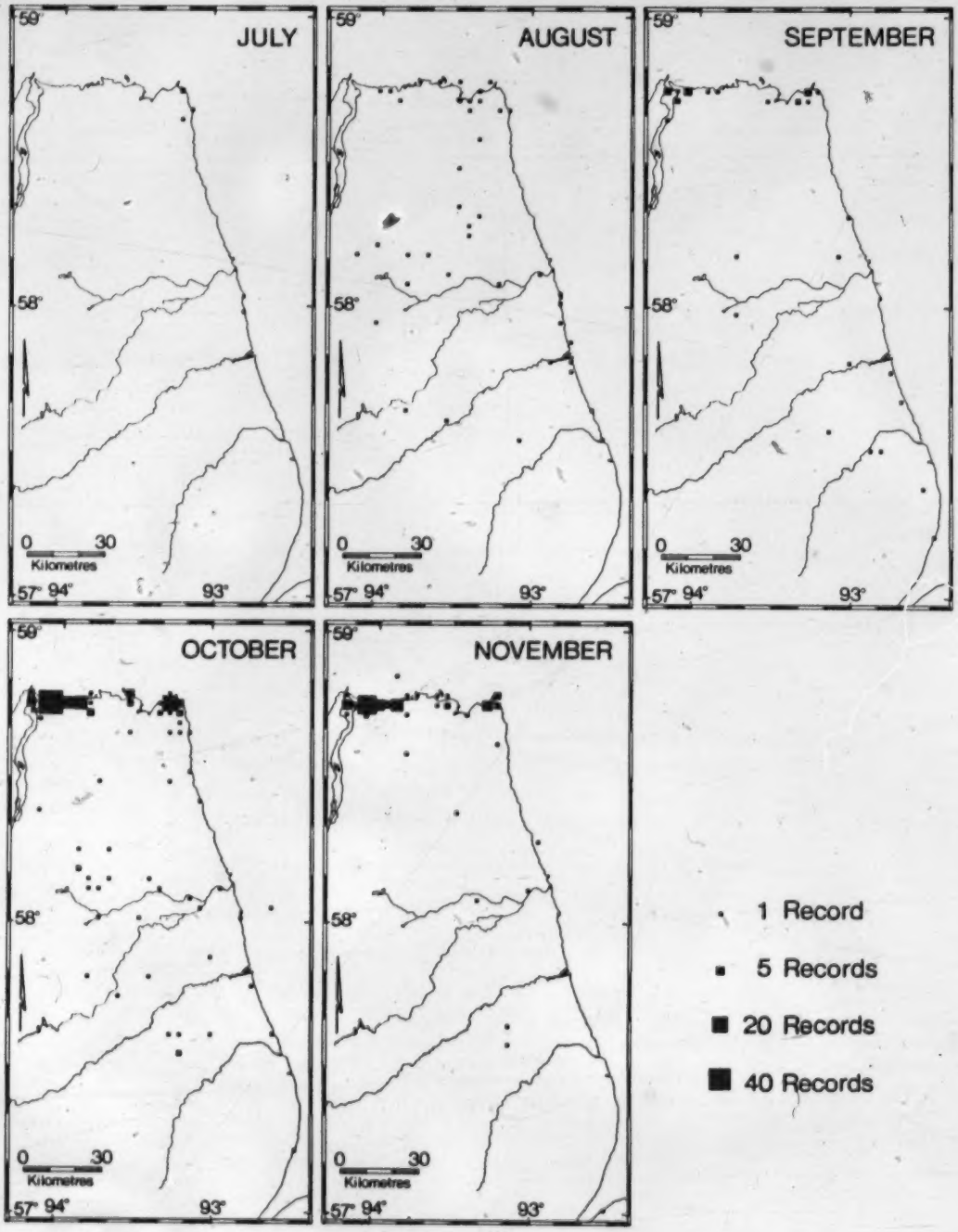

Figure 2-6. Map of monthly distribution patterns of subadult females, July through November, 1966-1985.

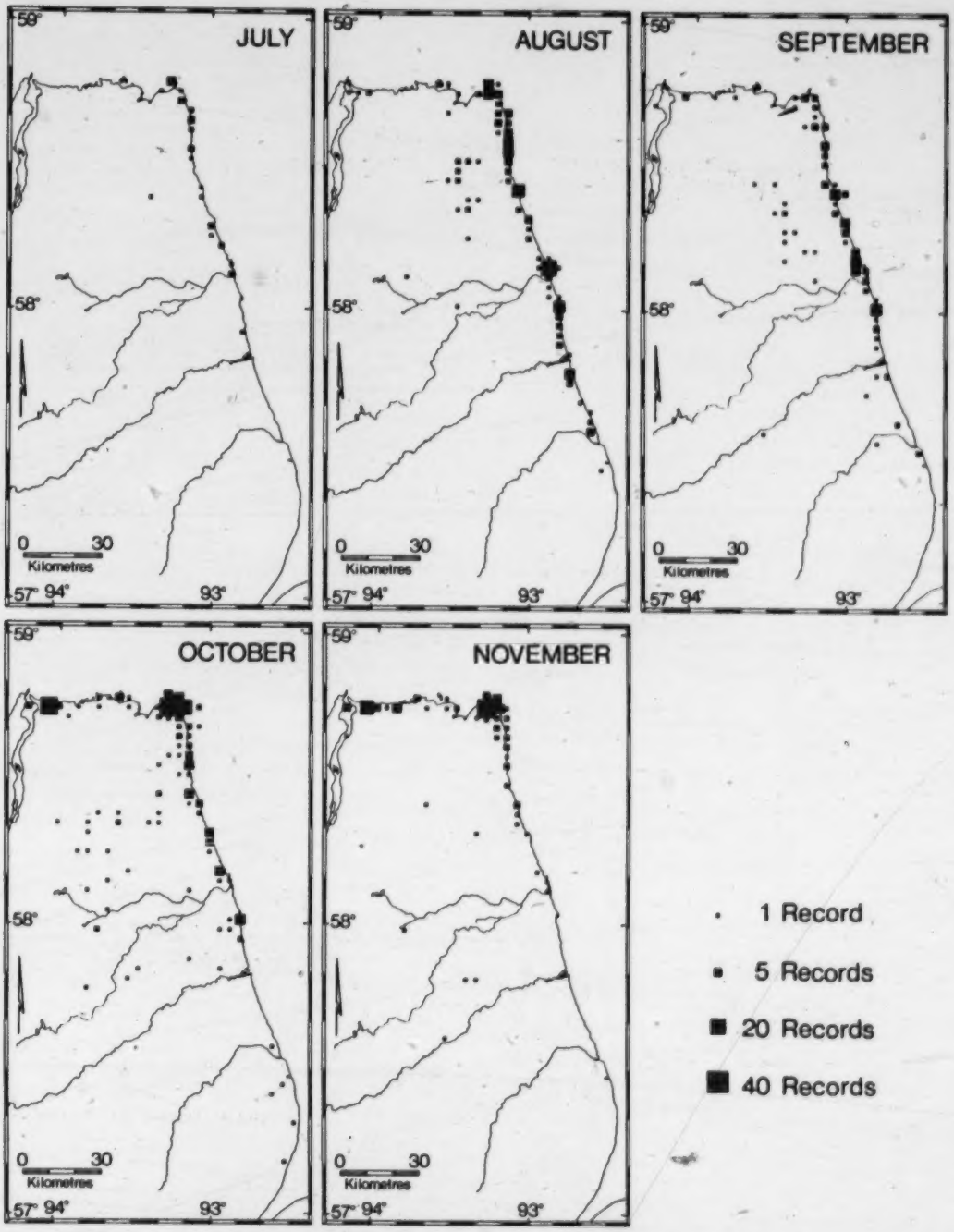

Figure 2-7. Map of monthly distribution patterns of adult males, July through November, 1966-1985.

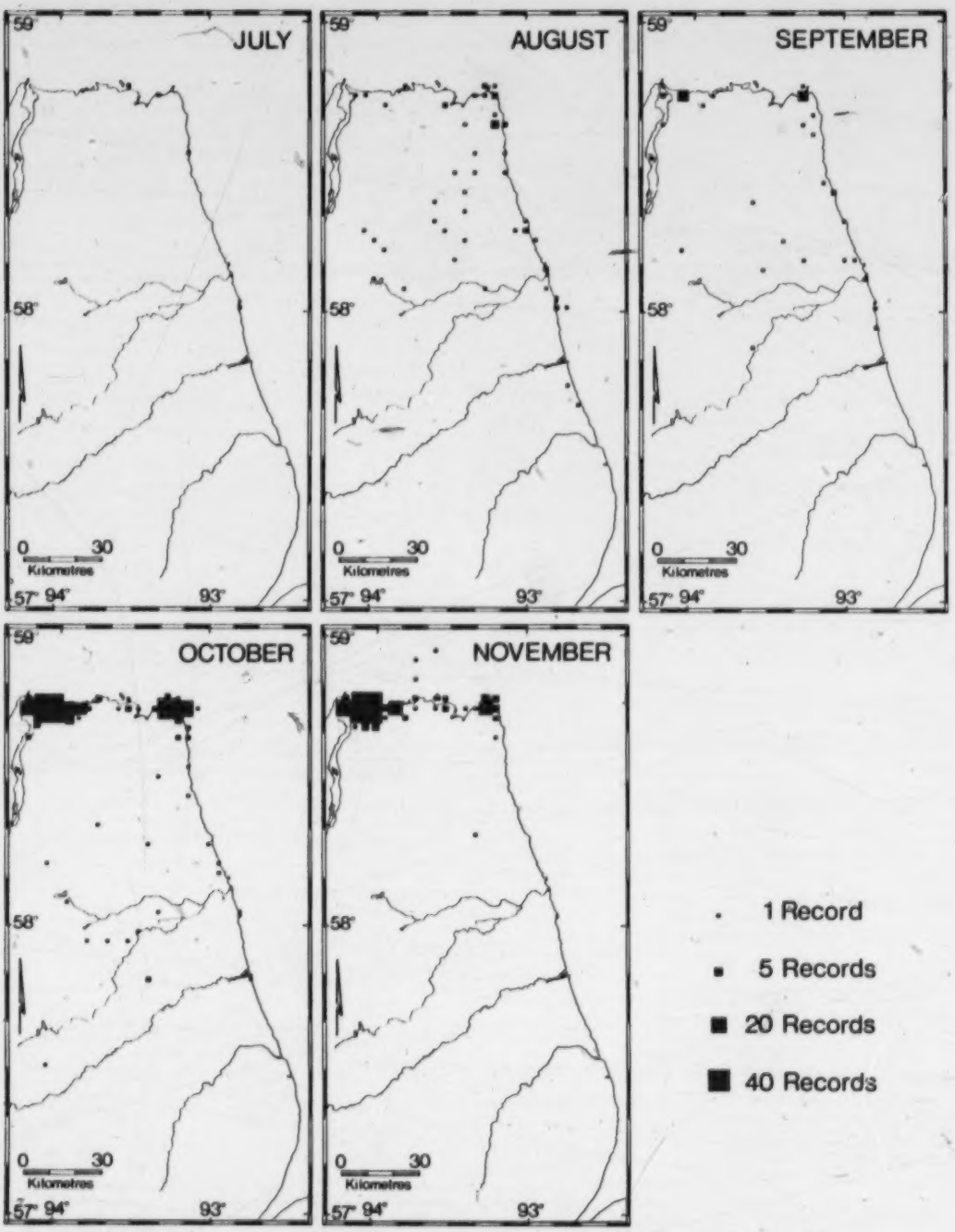

Figure 2-8. Map of monthly distribution patterns of subadult males, July through November, 1966-1985.

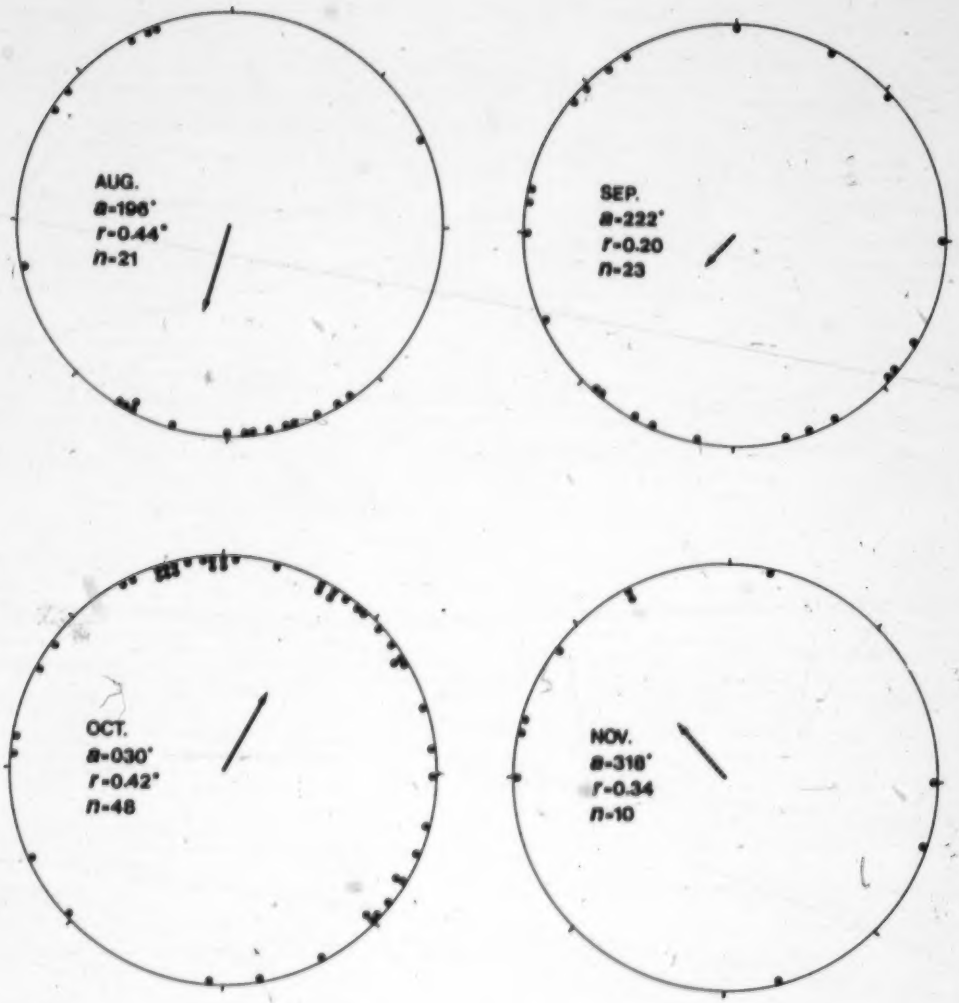

Figure 2-9. Orientation of movements by family groups by month. (* significant at $P<0.05$).

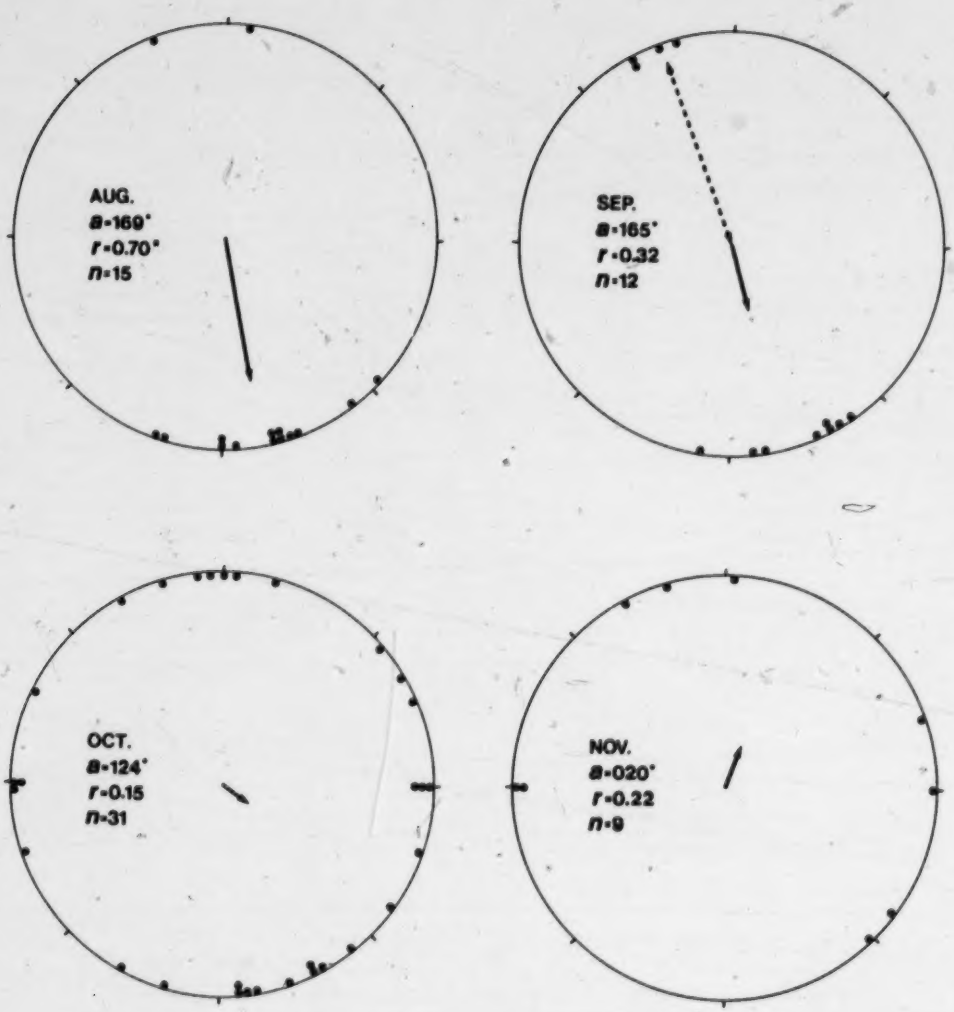

Figure 2-10. Orientation of movements by lone adult females by month. Dashed line indicates bimodal axis of orientation. (* significant at $P<0.05$).

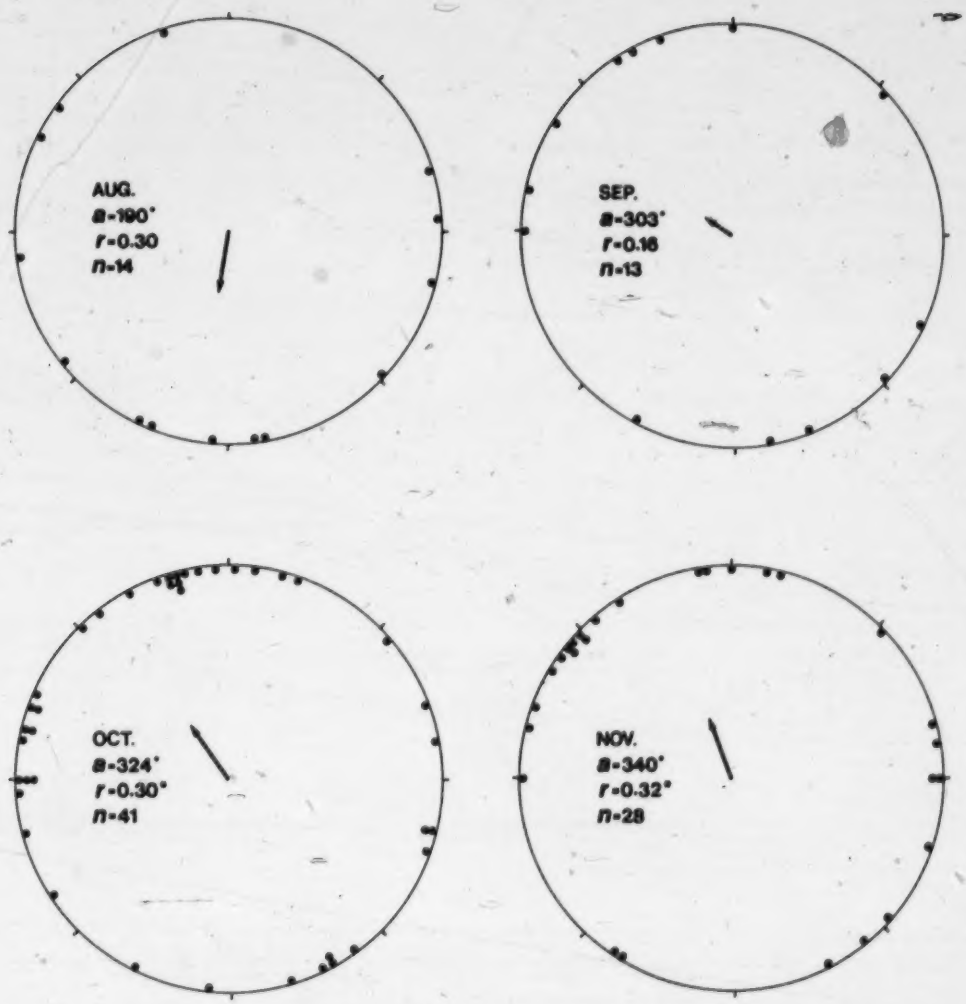

Figure 2-11. Orientation of movements by subadult females by month. (* significant at $P<0.05$).

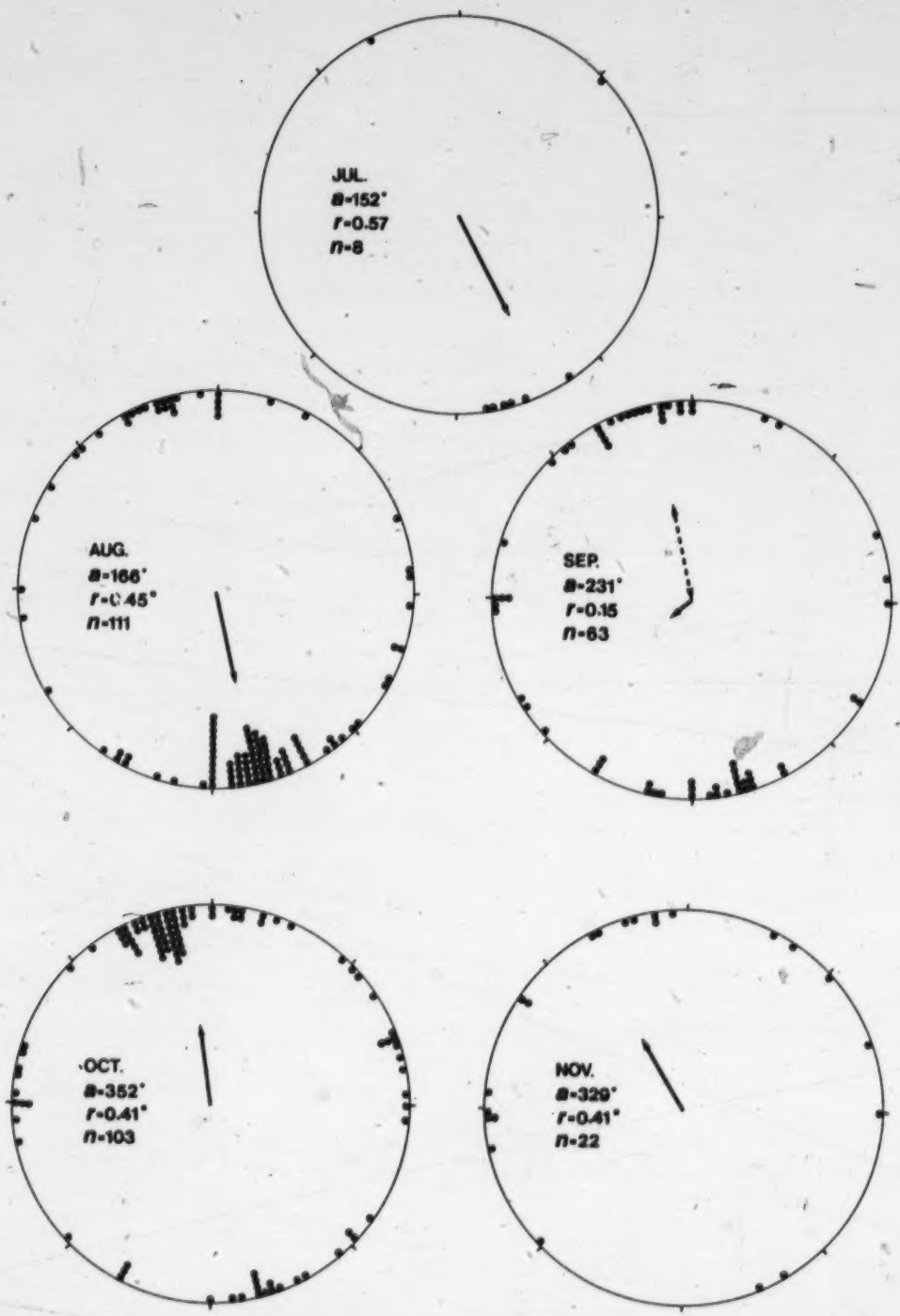

Figure 2-12. Orientation of movements by adult males by month. Dashed line indicates bimodal axis of orientation. (* significant at $P<0.05$).

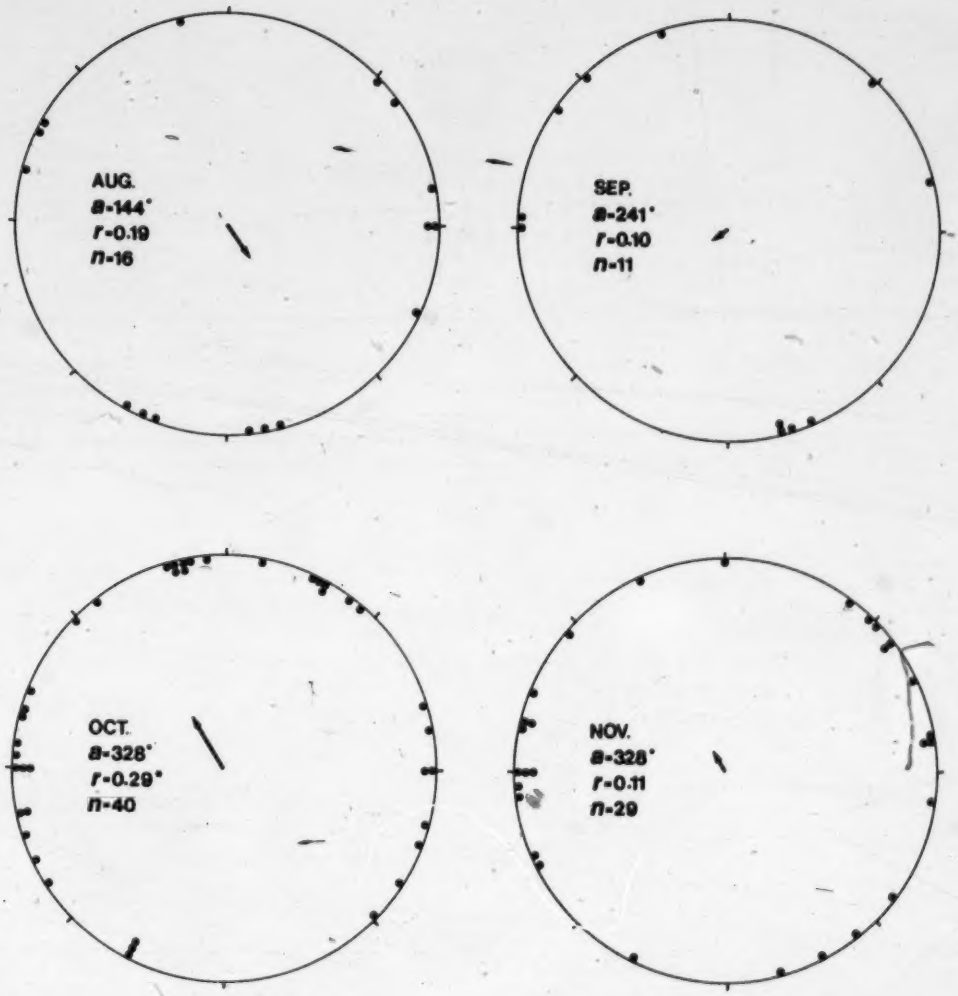

Figure 2-13. Orientation of movements by subadult males by month. (* significant at $P<0.05$).

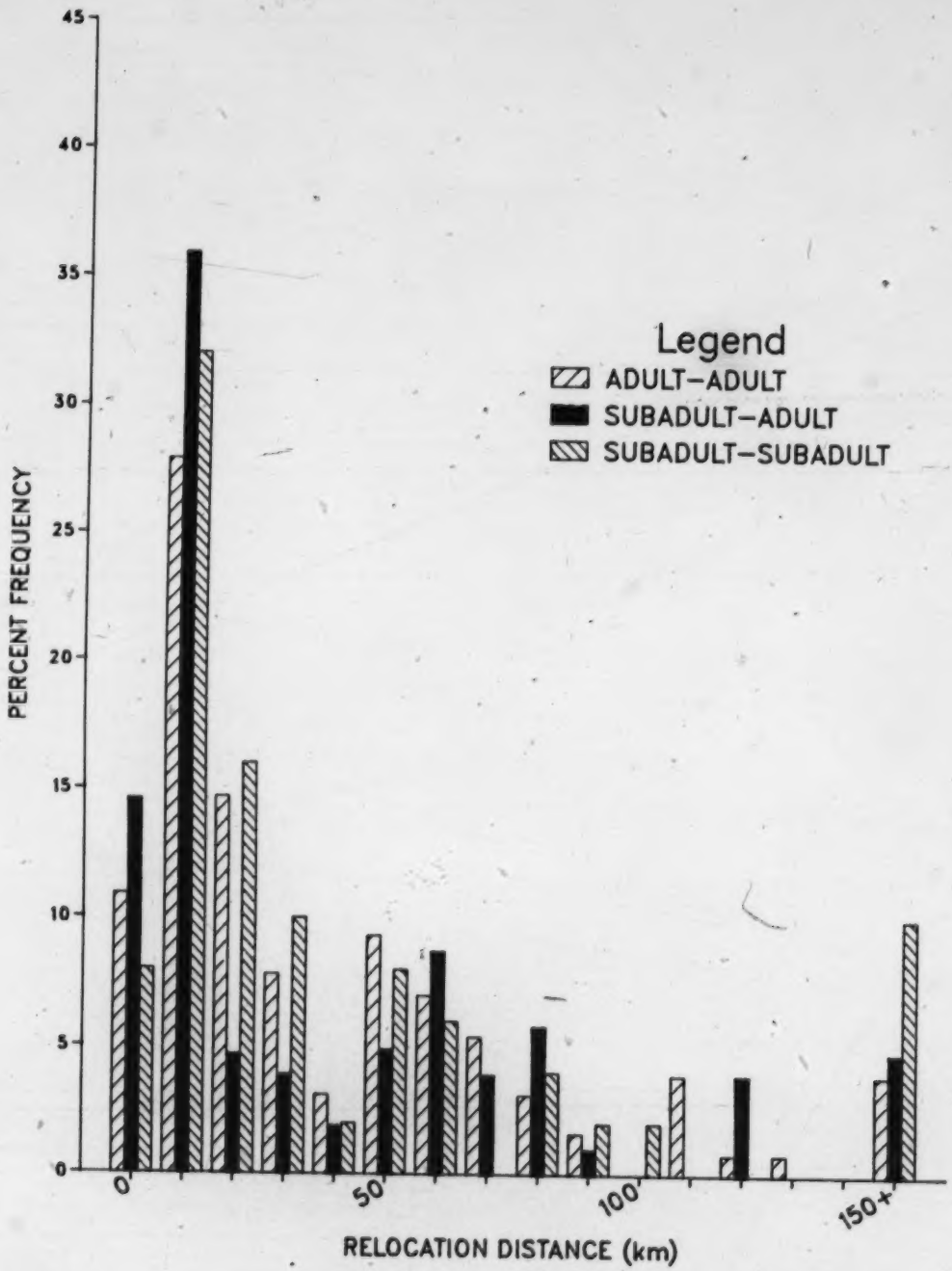

Figure 2-14. Histogram of percent frequency of relocation distances for adult females recaptured as adults (adult-adult), subadult females recaptured as adults (subadult-adult), and subadult females recaptured as subadults (subadult-subadult).

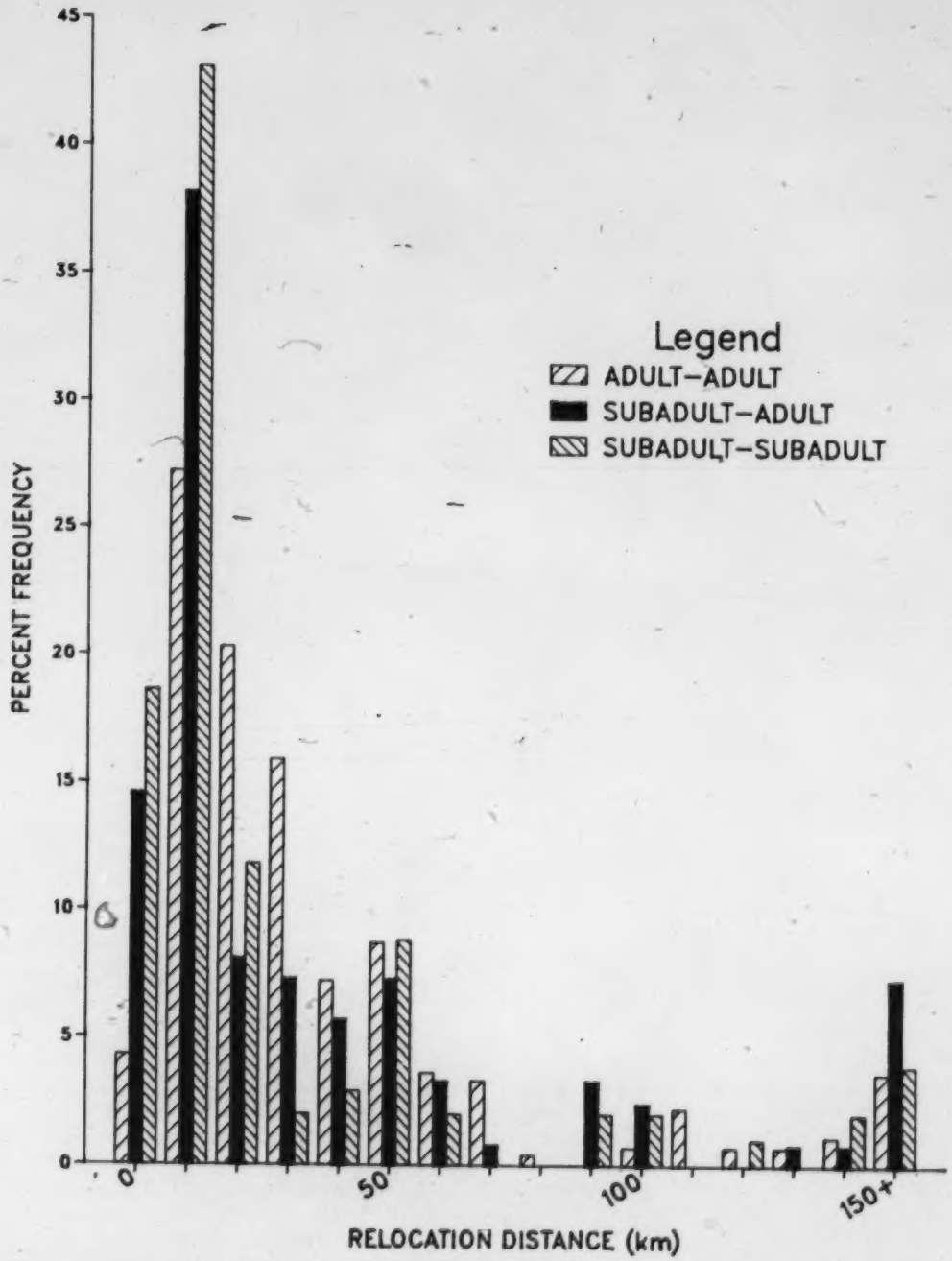

Figure 2-15. Histogram of percent frequency of relocation distances for adult males recaptured as adults (adult-adult), subadult males recaptured as adults (subadult-adult), and subadult males recaptured as subadults (subadult-subadult).

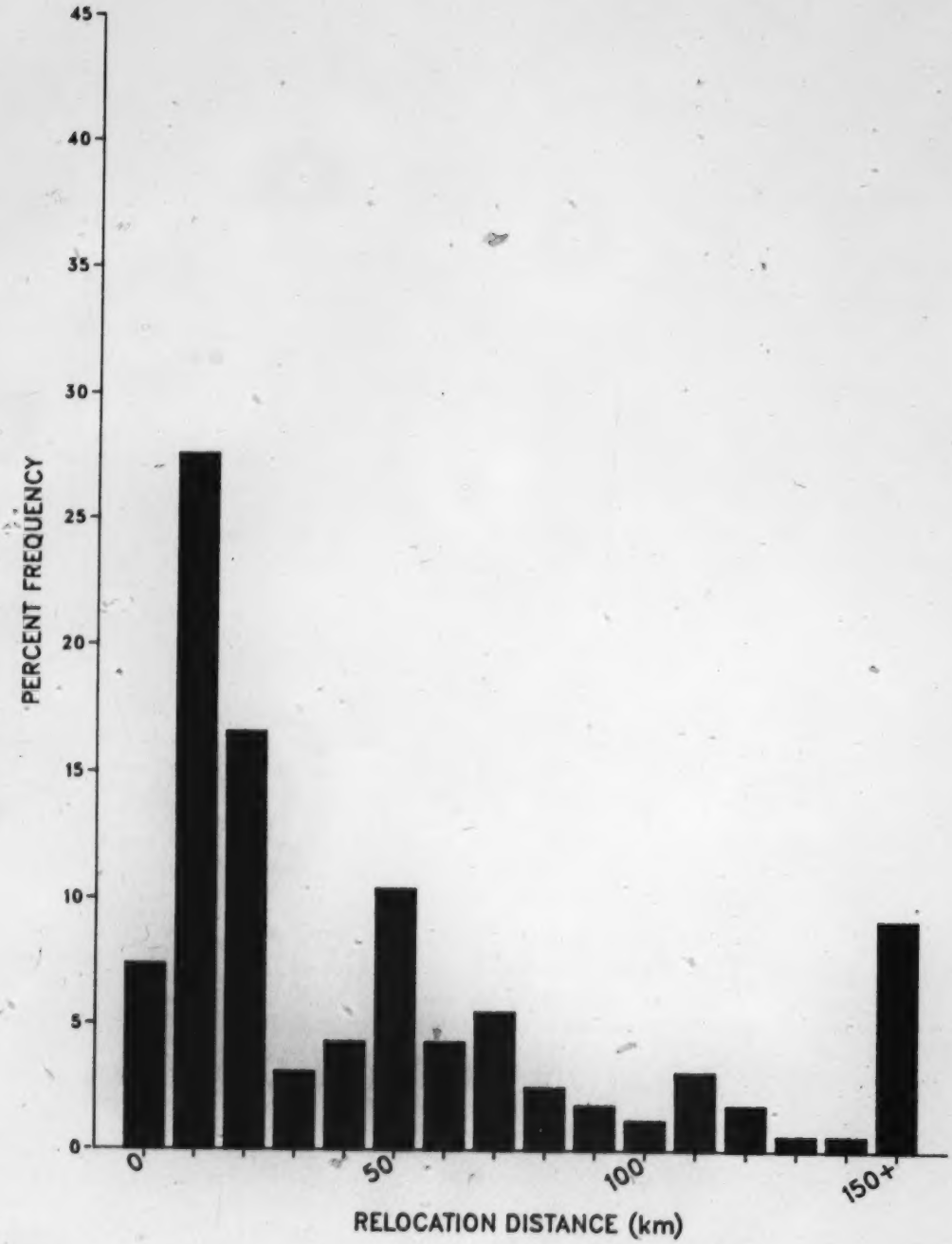

Figure 2-16. Histogram of percent frequency of relocation distances for cubs-of-the-year and yearlings with their mothers and subsequently located as independent animals.

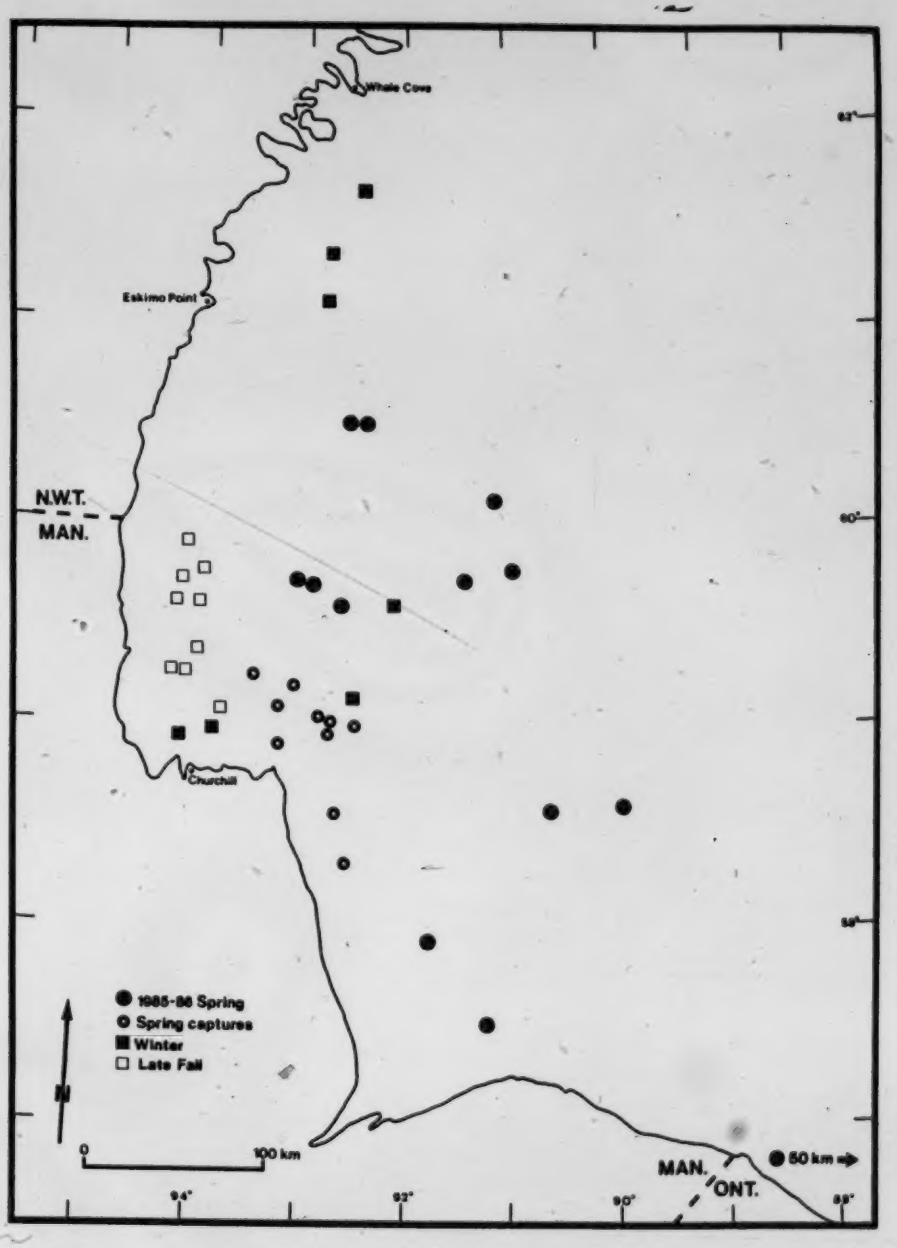

Figure 2-17. Map of western Hudson Bay showing locations of known polar bears on the sea ice.

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3. MARK AND RECAPTURE POPULATION ESTIMATE AND AERIAL CENSUS OF POLAR BEARS (*Ursus maritimus* Phipps) DURING THE ICE-FREE PERIOD IN WESTERN HUDSON BAY

3.1 Introduction

The quantification of animal abundance is a primary consideration in the study of ecology and estimates of population size are usually made using mark and recapture methods or aerial census techniques. However, the size of a large mammal population is often difficult to estimate because of the expense of marking individuals, large areas, low densities, logistic constraints, variation in behaviour making compliance to model assumptions difficult to achieve, and problems associated with detection.

Populations of polar bears (*Ursus maritimus*) have been estimated using multi-year mark and recapture models (Stirling *et al.* 1975; DeMaster *et al.* 1980; Furnell and Schweinsburg 1984; Amstrup *et al.* 1986). The estimates have often had large variances due to small sample sizes and low probability of recapture. Censuses done from the air or ships have been used to estimate polar bear population size in the Svalbard area (Larsen 1984). Amstrup *et al.* (1986) derived density estimates based on aerial surveys and reported on a single-season mark and resight estimate. Tovey and Scott (1957) and Prevett and Kolenosky (1982) used aerial surveys to develop population estimates or indices of abundance.

Polar bears are circumpolar in their distribution and are associated with the ice-covered arctic and sub-arctic seas. The distribution of polar bears is closely tied to the distribution of their major prey, the ringed seal (*Phoca hispida*), and to a lesser degree the bearded seal (*Erignathus barbatus*) (Stirling and Archibald 1977; Smith 1980). Polar bears demonstrate seasonal fidelity to localized regions and the world population is composed of numerous sub-populations (Stirling *et al.* 1975, 1977, 1980, 1984; Jonkel *et al.* 1976; Furnell and Schweinsburg 1984; Lentfer 1983; Larsen *et al.* 1983; Amstrup *et al.*

1986; Amstrup 1986; this study, Chapter 2). The breeding season occurs during late-March to mid-June (DeMaster and Stirling 1981).

Polar bears in Hudson and James Bays, the southern extent of their range, are forced ashore each summer because all the sea ice melts during July and August. A portion of the subpopulation in western Hudson Bay spends the ice-free period between the mouth of the Churchill and Nelson Rivers (Chapter 2). During the ice-free period, the bears rely largely on fat deposits for energy although some feeding on vegetation and carrion does occur (Russell 1975; Knudsen 1978; Lunn and Stirling 1985; Chapter 2). The population is discrete with little immigration or emigration during the summer and fall and segregation by age, sex, and reproductive class occurs while the bears are ashore (Chapter 2). During November, all non-pregnant bears return to the sea ice to hunt seals. Pregnant females remain ashore, giving birth to cubs in late December or early January, and subsequently return to the sea ice in March or April (Harington 1968; Stirling *et al.* 1977; Ramsay and Stirling 1982).

Interest in the number of polar bears in Hudson Bay is pertinent to several ecological questions dealing with the productivity and population dynamics of a large arctic mammal near the southern extent of its range. Between 100 and 150 polar bears are removed annually from Hudson Bay by Inuit hunters and management activities. To adequately assess the impact of such a harvest, an accurate estimate of population size is essential. The objectives of this study were to estimate the size of the study population of polar bears using single-season mark and recapture methods and aerial survey techniques and to assess the relative merits of each method.

3.2 Materials and Methods

The study area consisted of the region between the mouth of the Nelson River (57° N latitude) to the mouth of the Churchill River (58° 45' N latitude) from the coast and islands west of longitude 92° 25' W and inland to the CN railway at about longitude

94° 10' W (Figure 3-1). The 16,352 km² area is an extensive open peatland along the boreal forest-tundra ecotone (Thompson 1968) and is characterized by poorly developed drainage patterns and numerous small lakes and ponds. Elevations range from sea-level along the coast to 300 m above sea level in the western areas with numerous raised beaches and eskers scattered throughout. Continuous open spruce (*Picea spp.*) forest is found in the northwest corner and southern quarter of the study area. Sporadic patches of spruce and deciduous trees and shrubs are found along rivers and lakes in the inland area. Details of vegetation patterns are available in Ritchie (1960, 1962).

Polar bears were captured or marked from a Bell 206B helicopter using remote injection or marking equipment (Cap-Chur, Palmer Chemicals Ltd., Douglasville, Ga.). Capture techniques were similar to those used by Lentfer (1968) and Larsen (1971) with modifications outlined by Ramsay and Stirling (1986). The sample design of the captures and marking was based on a stratified random sample modified by constraints imposed by field logistics. Immobilized bears were marked with individually identifiable letters (30 cm high) along the back using an indelible black dye (Nyanzol). Other bears were remotely marked using 15 ml marker darts with the same dye. The marker darted animals were hit one to three times to ensure that a highly visible mark was evident along the upper portion of the back. Marker darts produced a large (15 cm diameter) mark that was variable in shape, but easily distinguishable from the air. Capture and marking of animals took place from July 26 through September 1, 1985. Bears were marked throughout the study area, roughly proportional to density and distribution patterns observed during previous years. Early in the capture period, bears were marked along the coast as they arrived off of the sea ice. However, as the residency time in the coastal area varies for different age and sex classes (Chapter 2), it was necessary to mark animals throughout the area.

Aerial transects were flown over the study area on September 21-23, September 30 to October 3, and October 17, 1985. On November 2 and 3 a survey was flown over

the study area just prior to the departure of the bears to the sea ice. Radio telemetry information indicated that most of the bears had left the inland area so the survey was modified and 7 strips were flown parallel to the coast at roughly 3 km intervals. Survey flights were flown with the same high-winged, twin-engined Cessna 337, at a target elevation of 125 m above the ground, with an approximate ground speed of 150 km/hour. The same 3 observers and pilot were used for all but the last survey, when one observer was substituted. The two primary observers sat in the rear of the plane, while the right front observer acted as data recorder and observer. The pilot navigated. The study area was divided into four sectors, as strips running the whole width of the study area were likely to be interrupted by fog along the coast (Figure 3-1). Parallel strips were selected at random in each sector with the provision that no two strips would fall within 3 km of each other. East-west transects were flown over three quarters of the study area. In the north-west sector, north-south transects were flown during ferry flights between Churchill and transects further south due to budgetary and logistic constraints. As movement patterns in the fall are generally northward (Chapter 2), the surveys began in the northeast corner and progressed south to reduce the likelihood that animals would be counted more than once.

Practice transects were flown to familiarize observers with the image of a polar bear at the survey altitude. The numerous lakes and creeks throughout the study area and prominent coastal features enabled accurate navigation along selected transects. The position of each animal was marked on 1:250,000 scale maps as accurately as possible based on their position relative to the transect line and prominent geographic features. If it was not clear if an animal was marked or not, the animal was circled to determine this prior to returning to the transect. Additional animals spotted while circling to determine the marked status of an animal were not included in aerial transect analyses, but were included in mark and recapture analyses. Bears were categorized by the presence or absence of marks and the size and age of cubs in family groups was noted.

Individual animals were not classed by age or sex given the difficulty in identification from the air.

Statistical procedures follow those outlined by Sokal and Rohlf (1981). The heterogeneity G-test (G_H), the chi-square test, and ANOVA's were used to analyze the assumptions of the population estimation methods. The level of significance was set at $P \leq 0.05$. Some statistical tests were performed using BMDP (Department of Biomathematics, The University of California, Los Angeles) statistical software.

3.2.1 Petersen estimate

The primary objective of this study was to evaluate the potential use of a single-season mark and recapture model for estimating population size (N). The visual sighting of animals in the population was the method of recapture in this study. The Petersen model (Seber 1982) was used as it was thought that the study design met the necessary assumptions. Mark and recapture analyses generally follow those outlined by Seber (1982) and Begon (1979). Notation follows that of Seber (1982). Calculation of population size was made using the following formula:

$$N^* = ((n_1+1)(n_2+1)/(m_2+1)) - 1 \qquad \text{(Chapman 1951).}$$

where:

N^* = population estimate,

n_1 = total number of bears marked at time 1,

n_2 = total number of bears seen on aerial surveys at time 2,

m_2 = total number of bears seen at time 2 that were marked at time 1.

For 7 or more recaptures this formula is virtually unbiased (Seber 1982). Chapman (1951) demonstrated that N^* is close to being the minimum variance unbiased estimator over the range of values for which it is almost unbiased. In order for N^* to be a reasonable estimator of N, a series of assumptions, not necessarily exclusive, must be met. These are:

1. The population is closed.
2. All animals have the same capture probability in the first sample.
3. Marking animals does not affect subsequent catchability.
4. The second sample is random.
5. All marks are permanent over the study period.
6. All marks are reported in the second sample.

The Petersen method is the simplest of mark and recapture techniques and as such has somewhat more restrictive assumptions than other models. Crucial to the analysis of the results of any mark and recapture model is an assessment of the assumptions and the possible biases that violation may produce.

An approximately unbiased estimate of variance (v^*), given by Seber (1982), was calculated for N^* using:

$$v^* = (n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)/(m_2+1)^2(m_2+2).$$

Approximate 95% confidence intervals of N^* were calculated using:

$$N^* \pm 1.96v^{*0.5} \quad \text{(Seber 1982).}$$

The number of dependent offspring in the population, cubs-of-the-year (COY) and yearlings, was estimated by using marked and unmarked family groups as population units to estimate the number of families. The number of cubs in the population was calculated as being the product of the number of families and the mean litter size. The mean litter size of both COYS and yearlings was estimated by using all of the information obtained during handling, marker-darting, and the September 30-October 3 survey. Begon (1979) recommended Bailey's (1951) formula for small recapture sizes:

$$\hat{N}_1 = n_1(n_2+1)/(m_2+1).$$

The terms are the same as the preceding formulae. The standard error of this estimate is:

$$v_1 = n_1^2(n_2+1)(n_2-m_2)/(m_2^2(m_2+2))^{0.5}.$$

The total population estimate was determined from the sum of the estimate of the number of independent bears and the number of dependent cubs. Minimum and maximum estimates were obtained by using the upper and lower 95% confidence limits of N^*, the number of families, and mean litter size. A weighted mean of the two surveys was calculated using the number of resightings (m_2) as a weighting factor following methods and variance estimate outlined by Begon (1979).

3.2.2 Aerial census

Strip transects were selected for the recapture method as the results could be used to obtain a second population estimate based on aerial survey methods. Analysis of aerial survey data follow methods outlined in Norton-Griffiths (1975). Kelker's method (Norton-Griffiths 1975; Eberhardt 1978) was selected to estimate the effective strip width after the survey was flown, as the distance to each animal could be estimated. Deviations from the strip were necessary to check for marks and and thus precluded a preset transect width. The strip width was determined by determining the fall off point in the number of animals seen as a function of perpendicular distance from the plane.

The calculation of the population estimate ($\hat{Y}$) and population variance follow Jolly (1969) and Norton-Griffiths (1975) for unequal sized sampling units. The following terms are used in the calculation of population size and variance estimates:

N = the number of sampling units in the population,

n = the number of sample units sampled,

Z = the size of the study area,

z = the size of a sampling unit,

y = the number of animals in a sampling unit,

$\hat{R}$ = the ratio of animals counted to area searched ($\Sigma y/\Sigma z$).

An estimated variance of $\hat{Y}$ was determined using:

$$\text{var}(\hat{Y}) = (N(N-n)/n)(s_y^2 - 2\hat{R}s_{zy} + \hat{R}^2 s_z^2).$$

where:

s_y^2 = the variance of animals counted in all units,

s_z^2 = the variance of the area of the sampled units,

s_{zy} = the covariance between the animals counted and the area of each unit sample.

The estimate of the total population is derived from:

$$\hat{Y} = Z\hat{R}.$$

The ratio of the number of radio tagged bears seen on the survey to the expected number of radio tagged bears, based on the proportion of the area surveyed, yields a rough estimate of detectability. The estimate is subject to several assumptions (*eg.* random mixing and sampling) and to errors associated with small sample sizes. However, it provides an indication of the proportion of the number of animals that may have been missed.

Caughley (1974) proposed an alternative method of estimating detectability using binomial probabilities. The framework of analysis is based on the observations of different observers. The basic concept is that: p = the probability that a given animal is seen by a given observer; p^2 = the probability that an animal is seen by both observers; $2p(1-p)$ = the probability that an animal is seen by one or the other observer; and $(1-p)^2$ = the probability that an animal is missed by both observers. The number of animals seen by a single observer is designated as S and the number seen by both is B. The value p can be estimated from the relationship:

$$2p(1-p)/p^2 = S/B$$

from which:

$$p = 2B/(2B+S).$$

This model must be modified to fit the circumstances of the survey performed, as it was not possible to determine which sightings were made by the two right observers. The assumption was that the number of animals on each side of the plane was equal and that observers did not vary in their ability to sight bears. From the aerial survey, the

frequency of observation from a single observer is available from the left side of the plane and is considered to be the number of animals seen by both observers on the right side. The number of animals that were missed by both observers (M) can be estimated from:

$$M = S^2/4B.$$

3.3 Results

Three attempts to fly strip transects over the study area were made during the fall of 1985, but the first two of the surveys could not be completed due to poor weather conditions. Only the September 30 to October 3 survey was completed. A modified strip transect was flown in early November.

3.3.1 Mark and recapture estimate

3.3.1.1 Validity of mark-recapture assumptions

1. *The population is closed.* It is generally assumed that the Petersen method provides an unbiased estimate of N only when additions and deletions to the population are non-existent or negligible. In fact, this assumption can be violated provided that rates of loss or gain of marked and unmarked individuals are similar.

In the Churchill population, during the ice-free period, additions to the population can only result from immigration of animals from outside the study area. Birth of cubs and disintegration of family groups occur during the winter and spring, respectively. The importance of immigration to the size of the study population, after the marking period, is inconsequential (Chapter 2). If immigration does occur, the Petersen estimate will apply to the number of animals in the population at the time of the second sample (Begon 1979).

During the ice-free period in western Hudson Bay, mortality of independent bears appears to be uncommon. Loss of cubs from family groups occurs while they

are on land and is reflected in the mean litter size only if part, but not all, of a litter is lost. Total litter loss would not affect the estimated number of family groups or the number of cubs, if mortality events were independent of marking. No cub mortalities were recorded in 1985. Two handling mortalities occurred during tagging procedures and were removed from n_1.

2. *All animals have the same capture probability in the first sample.* This is tantamount to sampling the population at random. It is difficult to determine if all animals have the same probability of capture in the first sample. All polar bears seen on a given day, within the allocated sampling area, were captured or marked. One possible indication of the nature of the sampling is to compare it against what might be expected. The sex ratio of polar bears at birth, in the study population, is 50:50 (Ramsay and Stirling 1987). While it is likely that differential mortality and possibly emigration may lead to a different sex ratio in the adult population, it does provide a reasonable comparison with the capture sample. The ratio of independent females and males in the capture sample was 42:58 (n=82) and was not significantly different from a 50:50 ratio (χ^2=2.56; P>0.1; d.f.=1). More sampling in the inland area was done by marker darting than by capture and as this is the area used by families and pregnant females, it is likely that the sex ratio of the total sample was close to even.

Variation in catchability between sub-groups in a population is a common violation of this assumption. The bias that is introduced into the estimate N^* can be reduced by using different trapping methods in the two samples (Seber 1982). Testing for variation in catchability requires a series of samples and examining the frequencies of recapture. As only two samples were completed in this study, this assumption cannot be adequately tested.

3. *Marking animals does not affect subsequent catchability.* Two methods of marking animals were used in the study; one involved drugging animals

while the second less perturbing method involved remote marking. In order to determine if the manner in which an animal was marked influenced the subsequent catchability (sightablity) of an animal, the percentage of individually marked (drugged and marked animals) in the recapture samples was compared to the original proportions. In the initial sample, 48% (82/172) were individually marked, not significantly different ($\chi^2=0.379$; $P>0.5$; d.f.=1) from the September-October sample with 44% (29/66) or the November sample with 45% (13/33) ($\chi^2=0.056$; $P>0.9$; d.f.=1). This indicates that the manner of marking did not influence the subsequent observability of marked animals, but does not conclusively show whether either method of marking influences future sighting.

Polar bears on land in autumn are generally highly visible as they are white objects on a snow-free background. No differences in behaviour that made marked animals more or less likely to be seen were observed. Marked and unmarked bears of all ages and sexes showed variable responses to the survey aircraft. In certain types of habitat (*eg.* open spruce forest) all bears were less visible, but in general all age and sex classes were equally visible in the September-October survey. During the November survey, most of the pregnant females were unavailable for recapture because they were in dens. If both marked and unmarked pregnant females are equally prone to being removed from the population available for sighting in the second population, then the proportion of marked to unmarked animals in the population should not change and the estimate N^* will still estimate N at the time of the first sample. This assumes that individuals of all different classes in the population were marked in the same proportion in which they occur. There was no apparent reason to believe otherwise. No individually marked bears were seen on more than one transect, indicating that sampling was without replacement.

In order to determine if different sub-groups in the population have significantly different catchabilities in the second sample, a chi-square test can be

used (Begon 1979). Using individually marked bears and marked family groups, the population was divided into five groups (*ie.* families, lone adult females, subadult females, subadult males, and adult males). The results of the chi-square test indicated that all five groups were equally likely to be caught in the second sample ($x^2=6.85$; $P>0.10$; d.f.$=4$).

4. ***The second sample is random.*** The second sample was a modified random sample and in reality it is difficult to know when a random sample, or an approximation of one, has been obtained. Systematic sampling can be used with the Petersen method if there is uniform mixing of marked and unmarked animals and all animals are equally catchable in the second sample (Seber 1982). While it is clear from Figure 3-2 and Chapter 2 that mixing of marked animals occurred, it was not possible to conclude that the animals were uniformly mixed. Inspection of Figure 3-3 indicates that there was variation in the ratio of marked to unmarked animals throughout the study area. In order to test for homogeneity in the distribution of tagged bears, the proportion of marked bears in the four sectors of the study area were compared. Going clockwise from the northwest, the proportion marked in each sector were 0.12 (4/32), 0.50 (42/84), 0.22 (14/64), and 0.26 (6/23). The differences were significant ($G_H=21.85$; $P< 0.001$; d.f.$=3$). The assumption of uniform mixing was violated and heterogeneity in the proportion marked did exist in different areas. Uniform mixing of marked and unmarked animals is preferred, but is crucial only if systematic sampling is used in the second sample. The sampling design used in this study was a modified random sample and while not truly random, should be sufficient to avoid serious bias. However, cautious interpretation of the results is warranted. The proportion of marked and unmarked family groups was not significantly different in the four sectors ($G_H=1.83$; $P>0.5$; d.f$=3$) and is indicative of uniform mixing for this group.

5. *All marks are permanent over the study period.* The dye used in the marking of bears is indelible and does not wash out, even from the hides of harvested animals commercially prepared. Of the 43 radio tagged animals marked in 1985, all of the 41 located during the ice-free period had fully visible and unaltered marks. Five bears, identifiable from radios or with marks from handling, were double marked with a total of seven marker darts, all of which were readily visible during subsequent sightings throughout the study period. Thus, the assumption that all marks were permanent over the study period is valid.

6. *All marks are reported in the second sample.* All bears sighted during the survey were closely examined at minimum safe airspeeds for presence or absence of marks. In instances where the marking status of an animal was not readily apparent, repeat passes over the animal were made until the status was confirmed. The dark dye and distinct markings used in this study contrasted strongly with the white pelage of the bears making misidentification unlikely.

The methods of marking were equally visible based on the proportion of the two types of marks that were present in the second sample. If individually marked animals were more likely to be classed as marked than the marker darted animals with smaller marks, then individually marked animals could be expected to be present in a higher proportion than they were placed in the population. The results presented earlier (see validity of assumption 3) indicated that both mark types were present in the proportions in which they were put out and that mark visibility differences were unlikely.

3.3.1.2 Petersen estimate

A total of 172 (n_1) independent bears, including 33 females with cubs, were marked during the capture and marking period. Of these animals, 90 were marker darted and 82 were marked with individually identifiable letters. Figure 3-3 shows the locations of marking. Two estimates of the population were made during this

study based on the resightings made during the aerial surveys (Table 3-1). The estimated proportion of the population marked ($\hat{p}=m_2/n_2$) was 0.325 (66/203) and 0.292 (33/113) from the September-October and November surveys, respectively. The data from the first two surveys were not analyzed due to incomplete coverage of the study area and small sample sizes.

The weighted estimate resulted in a population estimate of 544 (S.E.=55) independent animals in the population. This method is very similar to Schnabel's binomial model (Schnabel 1938; Seber 1982) which is essentially a weighted Petersen estimate.

Of 43 bears radio tagged in 1985, 13 were seen on the survey. If radio tagged bears are considered as a separate sample for analysis by mark and recapture methods then, using Bailey's (1951) formula, a population estimate of 627 (S.E.=156) independent bears was found.

The mean litter size was 1.46 cubs (COYS and yearlings) (S.E.=0.06) based on 68 different family groups (Table 3-2). There was no evidence of loss of cubs in marked or radio collared family groups during the ice-free period of 1985. The September 30 to October 3 survey produced an estimate of 101 family groups (S.E.=20) within the study area (Table 3-3). The second survey in early November produced an estimate of 116 family groups (S.E.=44) (Table 3-3). The weighted mean of the two estimates is 103 families (S.E.=24). A minimum of 68 different families were known to be within the study area during the ice-free period. Family groups represented 19.2% (33/178), 19.2% (39/203), and 11.5% (13/113) of the initial sample and the two recapture samples, respectively. These proportions were not significantly different (G_H=3.85; P>0.10; d.f.=3).

A minimum of 99 cubs were known to be present in the study area. Based on an estimate of 103 families and an average litter size of 1.46 cubs/litter, there were an estimated 150 cubs in the study area. Using the upper 95% confidence

limits for both the number of families and the mean litter size, the maximum number of cubs was estimated at 237.

The total population was estimated as the sum of the number of independent bears and the number of cubs. The total population size was estimated at 694 bears with minimum and maximum values of 535 and 889, respectively, using the weighted mean of the two surveys. Using the estimate derived from radio tagged bears, the total population size was 773 bears with a minimum of 420 and a maximum of 933.

3.3.2 Aerial census

The completed survey of September 30-October 3 resulted in a total of 2383 km of transect lines being flown in 29 hours of flying time. The mean coverage rate, including passes to check for marked bears, was 143 km/hr (S.E.=6, n=47). The November 2-3 survey covered a total of 1240 km of survey lines, although the data were not suitable for analysis using aerial census methods.

Data on the perpendicular distance of sighting were obtained for 94.6% (192/203) of the bears spotted. The remaining animals were either spotted after the transect was left or the distance to the animal was not recorded. Figure 3-4 shows the distribution of perpendicular sighting distance for bears seen during the September-October survey. Bears were spotted up to 3 km from the aircraft in some areas, but the overall mean distance from the transect was approximately 0.86 km (S.E.=0.06; n=192), excluding cubs in families. The distribution shows an abrupt drop in sightings beyond 1 km from the transect and thus the effective transect width was set at 1 km either side of the plane.

To test for differences in the number of observed bears between the right and left sides of the plane, the proportion of sightings were compared against an expected 50:50 ratio. The two observers on the right side of the plane saw 58.9% (109/185) of the bears while the left observer saw only 41.1% (76/185). Differences in the proportion

of animals spotted by each side of the plane were significant ($x^2=5.89$; $P<0.05$; d.f.=1).

If differences between the two sides of the aircraft are ignored, the total area surveyed was approximately 4,766 km², based on a 2 km wide transect (*ie.* 1 km per side). This represents approximately 29.1% (4,766 km²/16,352 km²) of the study area. A total of 168 bears were inside the defined transect, including 35 cubs. This resulted in a total population estimate of 576 with 95% confidence limits of 448 and 704.

Given that the left observer was missing substantially more animals than the combined efforts of the right observers, the estimate was recalculated using only the data from the right side. This produced a total population estimate of 734 bears (S.E.=105) with 95% confidence limits of 523 and 945. Approximately 14.6% (2,383 km²/16,352 km²) of the study area was surveyed using only the right observers. The detection profile did not change substantially using only the right observers.

Forty-three bears were radio tagged in the summer of 1985, of which 41 were confirmed to be present during the survey period. During the September-October survey, 23.3% (10/43) of these animals were seen within the 2 km transect. Given that 29.1% of the study area was surveyed, the expected number of radio tagged bears sighted should have been 12 or 13 (*ie.* 29.1% of 41 or 43). Sightability was estimated at between 77% (10/13) and 83% (10/12). The binomial method of estimating detectability was also calculated. An estimate of B from the left side of the plane was 76. As the combined efforts of the right observers was 109 bears, the number seen by a single observer S was then considered to be: 109-76=33. The probability that a given animal was seen by a given observer was estimated at 0.822. Using this value only an estimated 3.6 bears were missed on the right side of the plane and represented only 3.3% (3.6/109) of the bears seen.

The assumption that detectability was spatially homogeneous was tested with a one-way ANOVA, dividing the study area into three basic habitats: the open coast (less

than 10 km from the coast), the open inland, and the treed inland area. Although it seems likely that more animals were missed in the heavily treed areas than in the open tundra, no significant difference in the perpendicular sighting distance from the transect was found between the three areas (F=1.46; P=0.23; d.f.=2, 189).

To provide a basis of comparison of the different population estimates, the coefficient of variation was calculated and is presented in Table 3-4.

3.4 Discussion

The size of polar bear populations has been a primary concern since the First International Scientific Meeting on the polar bear was held in 1965 (Univ. Alaska 1965). The size of some populations has been estimated, largely through the use of multi-year population models (DeMaster *et al.* 1980; Furnell and Schweinsburg 1984; Amstrup *et al.* 1986). The population in western Hudson Bay is somewhat different than higher latitude populations, as the animals are present in much higher densities during the ice-free period and are more visible. The circumstances are such that a single marking session and recapture by resighting can be used in conjunction with a closed population model (*ie.* Petersen method). The use of aerial sightings as a recapture method has been used in mark and recapture population estimates in other large mammals (*eg.* white-tailed deer (*Odocoileus virginianus*) (Rice and Harder 1977)) and offers the benefit of reduced cost of recapture and improved compliance with random sampling assumptions.

The most reliable point estimates of size of the population in the study area are 694 and 734 for the weighted Petersen estimate and the transect estimate, respectively. The 95% confidence intervals were 535 and 889 for the Petersen estimate and 523 and 945 for the transect estimate. The Petersen method is moderately robust to some violations of the underlying assumptions (Seber 1982). The possibility that the assumption of equal capture probabilities was violated could not be ruled out. However, Mares *et al.* (1981) found that the Petersen method was more robust to violation of

equal catchability and in general, while the point estimate tended to underestimate population size, the confidence intervals consistently included the actual population size. Conversely, Strandgaard (1967) found that Petersen population estimates of roe deer were accurate only if two-thirds of the population could be marked. The major fault in Strandgaard's study probably lies in different probabilities of capture and recapture due to behavioural differences in sub-groups of the population. Robson and Regier (1964) recommended sample sizes of 200 for n_1 and n_2 to estimate a population of 1000 individuals for accurate management studies and samples of 400 for careful research into population dynamics. Given that the population size in the study area is roughly 700-800 individuals, the samples of 172 and 203 for n_1 and n_2, respectively, are sufficient for a reasonable estimate of population size.

Mark and recapture models in general tend to underestimate population size and instead often refer only to that portion of the population that is most easily caught. In this study, two different means of capturing were used in the two sampling periods and this may reduce some of the problems and biases associated with compliance with the assumptions. Using the Petersen method to estimate population size was partially dictated by the biology of polar bears during the ice-free season and logistic constraints that allowed for only one marking period, but the potential of several recaptures or resightings. Although the original study design allowed for four recapture surveys, poor weather conditions precluded the completion of two. This prohibited the use of some statistical tests of the data for compliance with the model assumptions. However, from the tests that were performed and prior knowledge of population characteristics and natural history, it appears unlikely that the assumptions of the model were significantly violated. Future Petersen estimates of polar bear populations should attempt to produce a more uniform distribution of marked animals in the population to reduce the possibility of violating model assumptions.

The population estimates from this study can be checked for consistency with what is known about the population from other sources. Table 3-5 presents the estimated number of COYS in the population based on the estimated number of families using the Petersen estimate, the proportion of families with COYS, and the mean litter size of COYS seen during 1985. In addition, the number of COYS expected to be present during the fall for populations of varying sizes are also estimated. Ramsay and Stirling (1987) reported a mean litter size of COYS in the fall of 1.60 COYS/litter (S.E.=0.05; n=113) and if this value is used instead of 1.46 COYS/litter found in 1985, the cub production from the population estimate is 122. This method is subject to several assumptions with respect to various population parameters. Ramsay and Stirling (1987) reported that females begin reproducing at 5 years and appear to be reproductively senescent at about 20 years. Based on age structure data collected from 1966 to 1985, 42% (357/852) of females are between 5 and 20 years of age. The natality rate of females in the autumn is 0.9 cubs/female/year for ages 5 through 20 years (Ramsay and Stirling 1987). This method, while only approximate, indicates that a population estimate of 700 polar bears produces roughly the same number of COYS as found from the Petersen estimate of the number of families. All of the parameters used in the analysis have some degree of variability and both means of estimation have wide variances.

Based on the sightings of families and tracks from 1970-1976, Stirling *et al.* (1977) estimated that approximately 82 family groups (S.E.=9; n=8), with 156 COYS (S.E.=17; n=8), were in the study area in the spring. Ramsay and Stirling (1987) reported a net mortality of 0.38 between the spring and summer/autumn. Based on this mortality rate and the Stirling *et al.* (1977) estimate of annual spring cub production, there should be approximately 98 COYS in the study area during the autumn period. This is similar to that obtained from the Petersen estimate.

Aerial census techniques have been used to estimate population size in numerous large mammal populations (*eg.* Siniff and Skoog 1964; Erickson and Siniff 1963; Sinclair 1977; Eberhardt *et al.* 1979; Kingsley *et al.* 1985; Bonnell and Ford 1987). Equally voluminous in nature is the literature dealing with the methodology and the nature of bias in aerial surveys (*eg.* Caughley 1974; Robinette *et al.* 1974; Norton-Griffiths 1975; Eberhardt 1978: Burnham *et al.* 1985; Pollock and Kendall 1987). In general, due to low probabilities of sighting, populations of bears do not lend themselves to aerial census, although there are some exceptions (*eg.* Erickson and Siniff 1963; Amstrup *et al.* 1986).

Numerous variants of aerial censusing large mammals have been developed; *eg.* strip transect methods (review by Eberhardt 1978; Burnham *et al.* 1980). The basic problem of density estimation, using strip transect methods, is to define the detection function of animals, given that an animal's probability of being sighted is a function of its distance from the transect line. Kelker's method, utilized in this study, involves a subjective decision by the researcher to define the strip width, after sampling, based on sighting distances. This method is thought to perform well in instances where the detection function demonstrates a sharp drop, within which all animals are assumed to be sighted (Robinette *et al.* 1974; Eberhardt 1978). The detection function found during this study did drop suddenly at approximately 1 km from the strip, making the use of this method feasible. The sharp drop in sightings beyond 1 km may be a function of the bears having reduced avoidance behaviour beyond this range. During the ice-free period, polar bears are highly visible making aerial census feasible. However, bears on the sea ice are cryptic and thus aerial surveys are probably of limited utility.

It is highly probable that some bears within the defined survey width were missed. The general similarity of the detectability estimates indicates that a large proportion of the animals present are seen. However, behavioural differences between individuals and groups within the population result in variation in the detectability of some animals. In particular, pregnant females in dens are likely to be less visible than

most other bears although, several were seen on the survey.

Aerial strip transect methods appear to be a functional means of estimating polar bear populations under circumstances where the animals are at relatively high densities and are highly visible. Previous use of aerial survey of polar bears have only been able to provide rough indices of abundance (Prevett and Kolenosky 1982; Amstrup *et al.* 1986). Aerial coastal counts of polar bear populations along the Hudson Bay coast may be useful as an estimator of the relative abundance of the polar bears. However, adult males tend to predominate along coastal regions (Chapter 2) and their numbers may not accurately reflect population trends. The considerable daily and annual variation in counts seen by Prevett and Kolenosky (1982) make coastal counts difficult to interpret.

Future aerial surveys of polar bears during the ice-free period could probably be improved by stratifying transects, using optimum allocation, based on known distribution patterns. One of the objectives of this study was to evaluate the utility of aerial surveys as a method of population monitoring. Future surveys would probably be improved if they were performed independent of mark and recapture estimates. Combination of the two estimation techniques was applied in this study largely due to logistic and financial constraints. Marker darting animals provides an unobtrusive and inexpensive means of marking animals for mark and recapture studies. The results indicate that future applications of this method are promising. Surveys as a recapture method or for strip transects should be done during September or early October; after all the bears are ashore, the ground is snow free, and the leaves on shrubs and trees have begun to drop.

The Petersen and strip transect methods appear to be viable options as an alternative to multi-year estimates under conditions where the detection of bears is sufficient. As the ratio of marked to unmarked animals should not be affected by detectability, the Petersen method may be applied to areas where animals are less visible, if the necessary assumptions are met. Which of the estimates yield the more reliable estimate is difficult to assess. The coefficient of variation from multi-year population

estimates of polar bears range from approximately 0.373 (Furnell and Schweinsburg 1984) to 0.447 (DeMaster *et al.* 1980). Coefficients of variation from this study are considerably lower than other methods and the single season methods used offer the additional benefits of being less expensive and requiring less time. Although the Petersen method costs more to undertake and requires the use of a helicopter, a reasonable estimate of the population size is possible if the necessary assumptions are met. Strip transect methods on the other hand are less expensive and require less manpower. The similarity in the estimates indicates that both methods are reasonable alternatives in circumstances similar to those found in the study area.

A population of 700-900 bears appears to be able to produce the estimated number of COYS in the study area and indicates that the estimates are in general agreement with what is understood about population structure and reproductive patterns. However, the estimates presented are only reliable to the extent that the underlying assumptions of both methods are met. It was possible to critically analyse only some of the assumptions and for most, compliance seemed likely or adequate. However, some assumptions were not or could not be adequately scrutinized and the possibility that biases were not present could not be confirmed. In conclusion, further estimates of polar bear populations should probably try to utilize as many sources of information and independent methods as possible to monitor trends in population size and productivity.

Table 3-1. Population estimates of independent polar bears in the study area.

Date	n_1	n_2	m_2	N^*	$v^{*0.5}$	Confidence interval[1]
Sep. 30-Oct. 03	172	203	66	527	41.0	447-607
Nov. 2-3	172	113	33	579	73.6	435-723

[1] $N^* \pm 1.96(v^{*0.5})$

Table 3-2. Litter sizes of all polar bear families seen in the study area during August-September, 1985.

Sample type	Adult females with 1 COY	2 COY	3 COY	1 Yrlg	2 Yrlg	Total
Handled	5	4	1	2	0	12
Marker dart	10	7	0	1	4	22
Unmarked	15	11	0	5	3	34
Total families	30	22	1	8	7	68
Total cubs	30	44	3	8	14	99

Table 3-3. Estimates of the number of family groups in the study area.

Date	n_1	n_2	m_2	$\hat{N}$	$v_1^{0.5}$	Confidence interval[1]
Sep. 30-Oct. 3	33	51	16	101	20	63[a]-139
Nov. 2-3	33	13	3	116	44	30[a]-202

[1] $\hat{N} \pm 1.96(v_1^{0.5})$

[a] there were at least 68 different families in the study area.

Table 3-4. Coefficient of variation of population estimates.

Estimation method	Coefficient of variation
Petersen estimate:	
Sep.-Oct. survey	0.078
Nov. survey	0.128
Weighted estimate	0.101
Families Sep.-Oct.	0.198
Families Nov.	0.379
Weighted estimate families	0.233
Radio tagged bears	0.249
Aerial transect surveys:	
Both sides	0.110
Right side	0.143

Table 3-5. The number of cubs-of-the-year in the population from population estimates and from populations of varying sizes.

Number of COYS based on estimated number of families	Number of COYS based on population size
number of families[a]: 103	hypothetical population size: 700
% of families with COYS[b]: 74%	sex ratio: 50:50
number of families with COYS: 76	number of females: 350
number of COYS[c]: 111-122	% of females reproductive age[d]: 42%
	reproductive age females: 147
	number of COYS produced[e]: 132

Estimated number of COYS from other population sizes

Population size	Number of COYS
500	94
900	170

[a] based on weighted Petersen estimate.
[b] based on Ramsay and Stirling (1987) and unpublished data.
[c] product of mean litter size and number of families.
[d] females reproductive between 5-20 years of age and age structure data (Ramsay 1986; Ramsay and Stirling 1987).
[e] natality rate 0.9 (Ramsay and Stirling 1987).

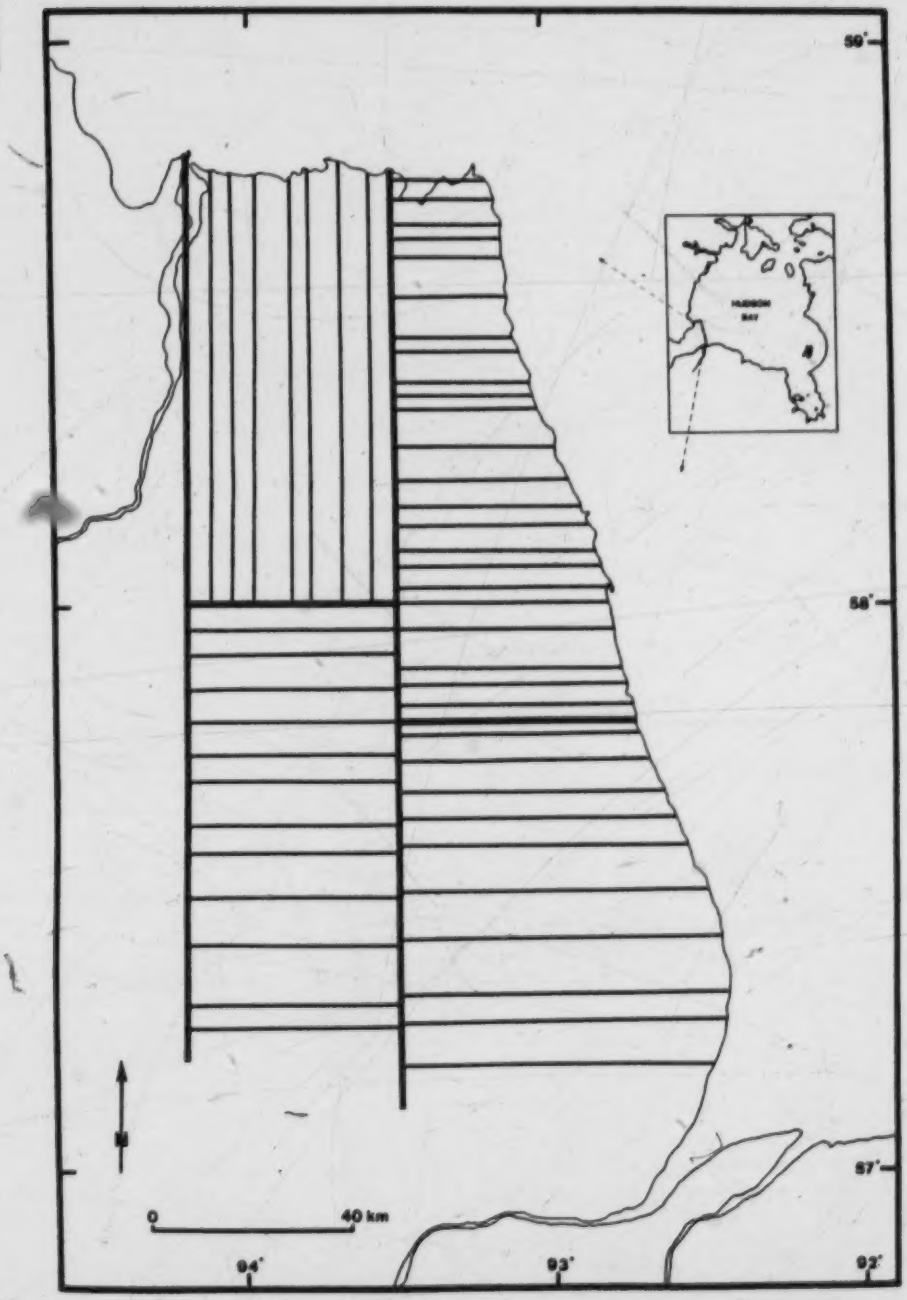

Figure 3-1. Map of study area showing aerial survey transects and sectors.

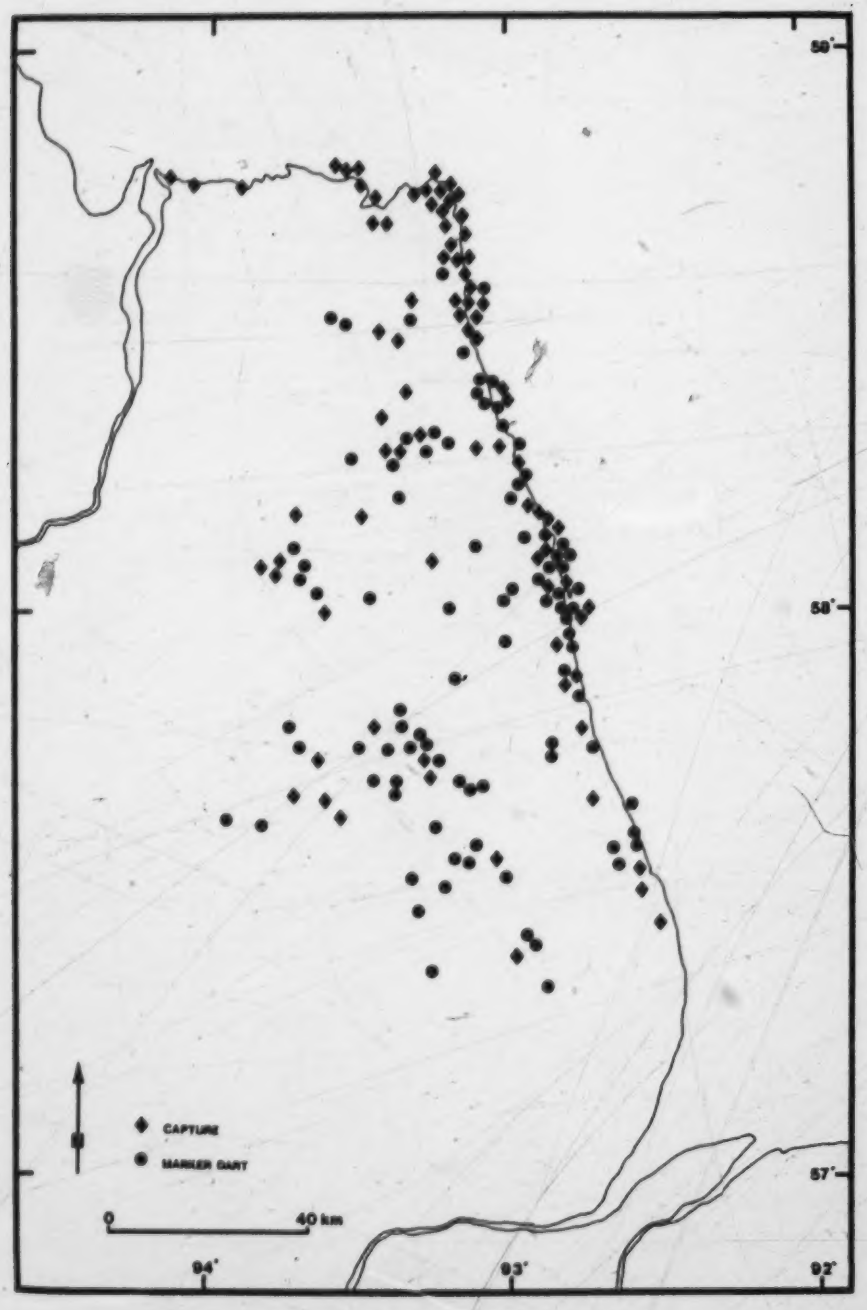

Figure 3-2. Map showing locations of polar bears handled and marker darted in 1985.

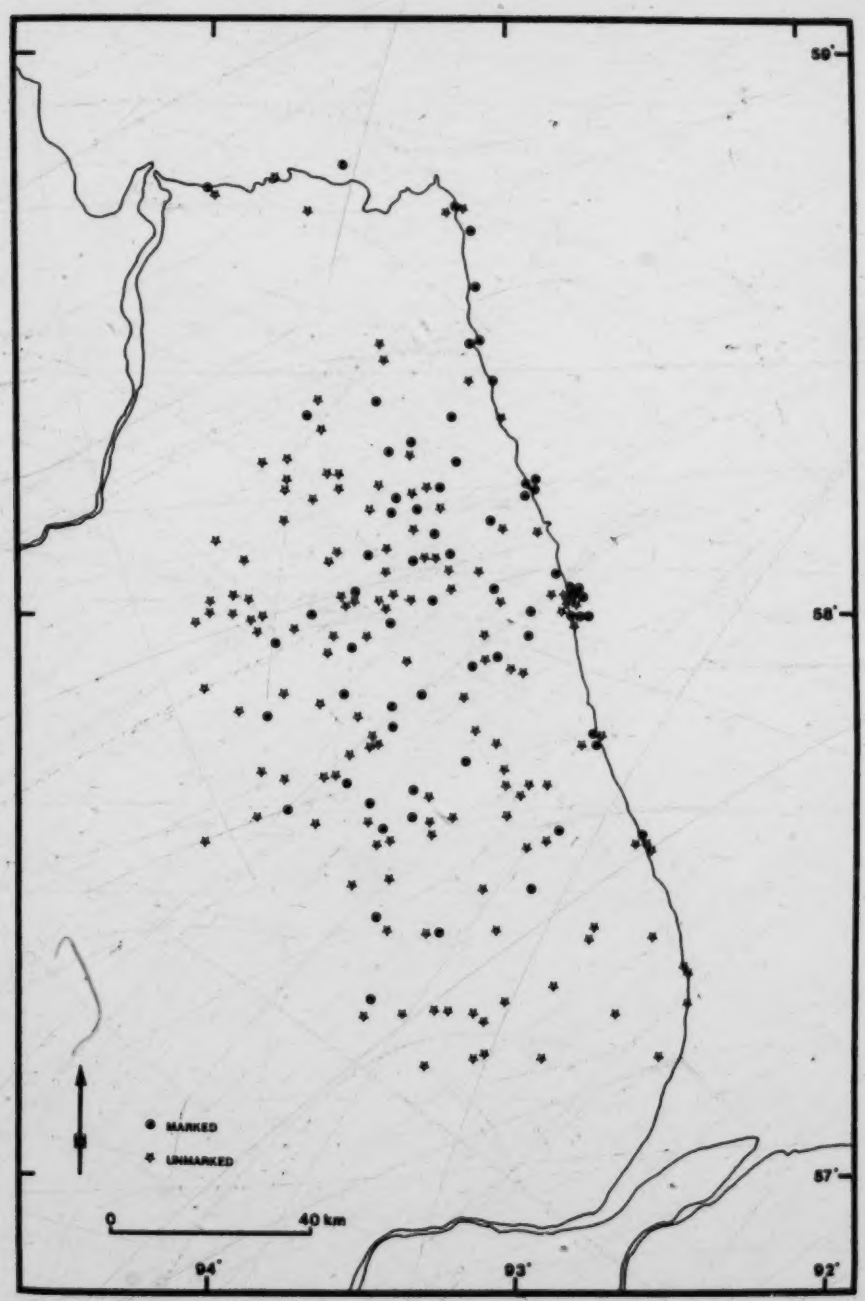

Figure 3-3. Map showing distribution of marked and unmarked bears seen during the September-October survey of 1985.

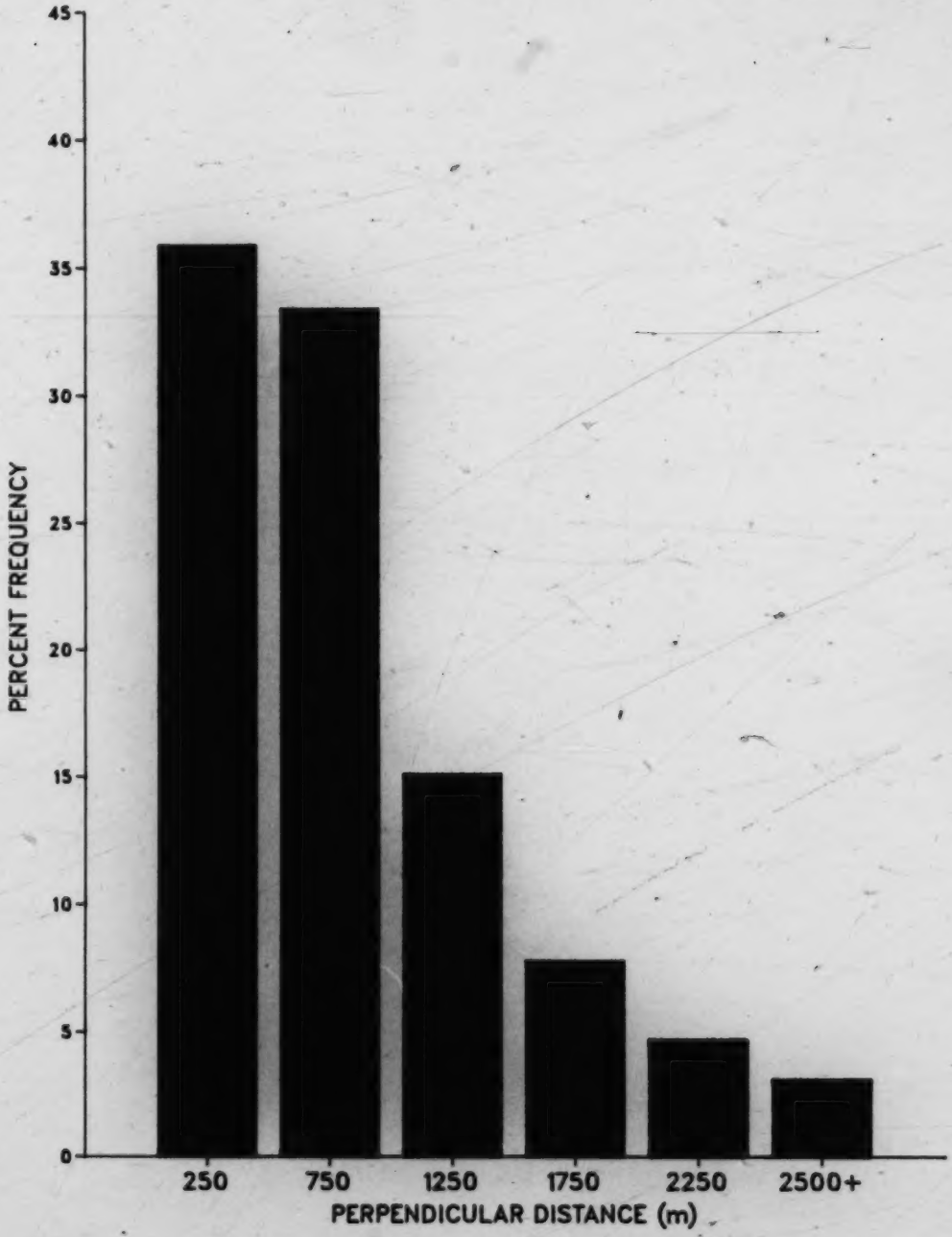

Figure 3-4. Histogram of perpendicular sighting distances of bears seen during the September-October survey, 1985.

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4. SUMMARY

The distribution, movement, and site fidelity patterns of polar bears during the ice-free period in western Hudson Bay are a function of several interacting social and ecological factors. The primary habitat of polar bears is the circumpolar arctic sea ice and the time spent in terrestrial habitats is a function of a forced migration due to the melting of the sea ice. Stirling *et al.* (1977), Latour (1981), and Lunn and Stirling (1985) have commented on aspects of the spatial and temporal segregation of the different age, sex, and reproductive classes of bears during the ice-free period. This study examines more extensively the patterns of distribution and movement during the ice-free period.

Bears of all age, sex, and reproductive classes were present along the coast throughout the ice-free period, but the region was predominantly occupied by adult males. Most family groups spent August through September in the inland areas. Adult females with cubs-of-the-year and yearlings were similar in distribution and movement patterns. Most lone adult females moved into the inland area soon after arriving on shore, but those found along the coast in October and November were lighter than those further inland and were thought to have insufficient fat stores to successfully produce and nurse cubs. Subadult females and males had similar distribution patterns and were found throughout the study area, but occupied different areas than other groups during some months. All groups of bears demonstrated monthly variation in distance from the coast, but the magnitudes were different. Once on land, patterns of segregation appeared to be similar to those noted by Stirling *et al.* (1981a) on the sea ice although some of the underlying influences appear different.

The spatial distribution of polar bears during the ice-free period cannot be explained completely by family groups avoiding adult males as suggested by Lunn and Stirling (1985) or by the threat of infanticide by adult males on cubs (Taylor *et al.* 1985). The ice-free period is two or three months after the breeding season and no

benefit, other than nutritional, could be obtained by infanticide. In addition, cubs are of sufficient size to outrun adult males by the ice-free period. The observed patterns appear to be related to several factors, of which the aforementioned are but two. The results of this study indicated that site fidelity to specific locations in the study area appeared to be involved in movement patterns. Low levels of immigration and emigration in the study population were found and may be a function of different hunting areas for the sub-populations in Hudson Bay and fidelity to areas nearby during the ice-free period. Within a single year, bears found in the study area tended to remain in the study area until freeze-up. While the sea ice demonstrates annual variability, recurrent patterns are common and are of major importance to polar bears and their prey (Stirling *et al.* 1981b). The ability to quickly locate or relocate good hunting areas is probably critical to the survival of polar bears. Site fidelity and movement patterns are probably related to relocating hunting areas on the sea ice. Equally important to polar bears is the ability to locate suitable areas to spend the ice-free period. There are indications from this study that, after weaning, subadults use the same areas and travel routes as they did when they were cubs following their mothers. This may be particularly important for female offspring when they subsequently seek denning sites as reproductive females, as the denning area in western Hudson Bay is much further inland than in most areas.

It was not possible to determine the importance of foraging during the ice-free period although evidence of feeding on *Vaccinium* spp. in the inland areas was found and may represent a relatively high quality and reliable food source for a brief time during the ice-free period. While berries do not represent as high a quality food source as seals, bears are opportunistic feeders and evidence of foraging and scavenging are not surprising.

Some of the aspects of segregation and movement in the population were consistent with the conservation of stored fat reserves. The amount of daily movement

by families, adult males, and subadult females was lowest during September. Suspected pregnant females reduced daily movement through the ice-free period as den sites were selected. Subadult males did not demonstrate monthly variation in movements. The magnitude of movements for all groups of bears were similar during the ice-free period and were substantially below those found on the sea ice. Spatial segregation of adult females with cubs may also function to conserve energy. By moving into the inland area, the probability of interacting with other bears is reduced, thereby lowering energy expenditure on defence, avoidance behaviour, and vigilance. Movement and distribution patterns were not strongly related to the age and weight of an individual although significant correlations were found for some groups in some periods.

Aggregating of adult males during the ice-free period is probably facilitated by the temporal distance of the breeding season, as circulating testosterone levels are lower than those found during the breeding season. Aggregations may form as the costs of associating are low and familiarity with conspecifics may reduce the frequency and severity of future conflicts over resources. The larger size of adult males in aggregations was considered to support the hypothesis that a loose dominance hierarchy, based on body size, exists in polar bears. Ursid social behaviour is not well understood although, the aggregating behaviour of adult males is a further example of the plasticity of carnivore social groups that have arisen from diverse selective pressures.

The direction of observed movements demonstrated recurrent patterns of orientation in movements to and from the areas used during the ice-free period and was considered evidence of navigating ability. Family groups moved inland and returned to the coast along an axis of orientation similar to that reported by Ramsay and Andriashek (1986) for families leaving the maternal denning area during the spring. Adult males tended to move southward along the coast in July and August and return northward in October and November. Other groups of bears were less orientated in movement patterns although movements parallel to the coast were also seen in lone adult females

and subadults. Overall, the population moved south early in the ice-free period and then returned north prior to freeze-up. This pattern was thought to be related to sea ice formation patterns allowing earlier access to hunting habitat. Variation in densities throughout the study area were thought to be related to habitat selection. No particular habitat or region was optimum for all bears as the requirements of the different groups were probably not the same.

While the polar bears of western Hudson Bay are concentrated on land, it was possible to utilize the higher densities and lower operating costs to obtain a population estimate of the number of bears in the study area in a single ice-free season. Two techniques were used to estimate the population size: the Petersen mark and recapture method and Kelker's strip transect method. The total population was estimated at 694 bears (95% confidence interval=535-889) and 734 (95% confidence interval=523-945) using the Petersen and strip transect methods, respectively. An analysis of the assumptions of the Petersen method showed that they were met or approximated. An understanding of the movement and distribution patterns of the study population was crucial to the testing of population closure.

An estimated 103 family groups (S.E.=24) were present in the study area. Between 99 and 237 cubs-of-the-year and yearlings, with a point estimate of 150 cubs, were estimated to be present in the study area. Of these, approximately 111 were thought to be cubs-of-the-year.

Overall, both methods produced similar estimates of population size and an analysis based on reproductive patterns revealed that a population of about 700 bears would produce the observed number of cubs-of-the-year. Both estimates had coefficients of variation lower than previous studies of polar bear populations.

The population of approximately 700 bears concentrated on land during the ice-free period in western Hudson Bay, between the Churchill and Nelson Rivers, demonstrate definite and recurrent patterns of distribution, movement, and site fidelity.

These patterns permit a large number of polar bears, a normally solitary species, to spend a non-competitive period of low food availability, at high densities and conserve energy stores. However, a more thorough understanding of the social interactions and behaviour patterns of polar bears, on and off the sea ice, is necessary before all of the observed patterns can be fully understood. Integrating information on the distribution and movement patterns of polar bears should enable future studies to more efficiently study the population dynamics and ecology of polar bears.

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